universität wien

DIPLOMARBEIT

Titel der Diplomarbeit

Picture-object recognition in a comparative approach:
Performance of humans (*Homo sapiens*) and pigeons (*Columba livia*)
in a rotational invariance and a complementary information task

Verfasserin

Mag.rer.nat. Anna Frohnwieser

angestrebter akademischer Grad

Magistra der Naturwissenschaften (Mag.rer.nat.)

Wien, 2013

Studienkennzahl lt. Studienblatt:	A 439
Studienrichtung lt. Studienblatt:	Diplomstudium Zoologie
Betreuerin:	Dr. Ulrike Aust

ACKNOWLEDGEMENTS

First of all I would like to thank Claudia Stephan and Ulrike Aust for their supervision and support. Furthermore I want to thank everybody working in the pigeon lab for their input, chats, and coffee breaks, with a special thanks to the animal caretakers!

Thanks to my mother, who supported me not during one but during two diploma theses, and to the rest of my family and friends, who were there for me during these last few years!

TABLE OF CONTENTS

I. INTRODUCTION

For many species vision is the primary sensory system to perceive the world around them. This involves navigation, foraging, recognition of conspecifics and predators, habitat selection, and many more aspects crucial for survival. In the present study the focus was on object recognition. Two highly visual species – pigeons and humans – were investigated to find out whether they can recognize new rotational views of familiar objects. Furthermore, pigeons were tested on two complementary information tasks to investigate their understanding of pictures as representations of real-life objects.

1.1. Visual systems of pigeons and humans

Pigeons and humans are two highly visual species that have evolved separately for about 310 million years (Kumar and Hedges, 1998). While ancestral mammals were largely nocturnal, ancestral birds were diurnal and aerial and therefore had very different visual needs, resulting in divergent evolution (Walls, 1942). After the saurian mass extinction 68 million years ago, many mammal species evolved back from a nocturnal to a diurnal lifestyle (Walls, 1942). Today, most birds and mammals use vision for navigation, foraging, and recognition of conspecifics, and therefore share functional similarities due to convergences. However, the biological structures involved in vision differ greatly between the two groups. While birds have a reptilian, midbrain-based visual system, the mammal visual system is forebrain-based. Furthermore, the retinal structures of birds and mammals differ greatly. Placental mammals possess only single cones, while birds' retinae possess single cones and double cones, which can contain oil droplets that may relate to the ability to perceive very short spectral wavelengths such as ultraviolet or near ultraviolet light (Husband and Shimizu, 2001). Humans are trichromatic, i.e. possess three different cone types to perceive color, with

sensitivity maxima at 440, 535, and 565nm. Pigeons are pentachromatic or tetrachromatic (Cuthill and Bennet, 1993). They have sensitivity maxima in the spectral region visible for humans (460, 530, and 595nm), and another maximum in the near-ultraviolet region (365-385nm) which is not visible for humans (e.g. Cuthill et al., 2000; Emmerton and Delius, 1980; Remy and Emmerton, 1989; Romeskie and Yager, 1976). Pigeons are also sensitive to polarisation which may enhance the perception of surface reflections (Delius et al., 1976).

Because of the lateral position of their eyes pigeons mainly rely on monocular vision and use true binocular stereoscopy only when they approach, fixate, and peck at objects from a distance of about 30cm (Goodale, 1983; McFadden, 1993). When flying through narrow or obstructed space monocular information about depth must be essential for navigation; therefore, other depth cues such as occlusion patterns, perspective size, texture gradients, shading patterns, and accommodation efforts must be used. It has been shown that pigeons are sensitive to such depth cues in pictorial stimuli (Cavoto and Cook, 2006; Cook et al., 2012; Reid and Spetch, 1998).

1.2. Picture-object recognition

1.2.1. Levels and experimental evidence

Even though a great number of studies have been conducted using pictures as stimuli to find out more about pigeon cognition, it is not easy to determine how pigeons perceive two-dimensional stimuli such as photographs, computer images, or movies. Photography, computography, and videography are all based on human trichromatic vision (three basic colors mixed), but for pigeons four or five basic colors would be needed to create all colors they can see. Furthermore, flicker, movement, and depth cues in photographs and videos are designed to recreate a realistic image only for the human eye, and auditory and olfactory cues are missing (see D'Eath, 1998 for a review).

Fagot and colleagues (2000) describe three main modes to identify what a person or animal perceives when looking at a picture that represents an object:

1) *Independence mode*: No association is formed between objects and their pictures, as both are processed independently via shape, color, and other features.
2) *Confusion mode:* Pictures and objects are processed in exactly the same way and therefore treated the same way, for example animals trying to grab and eat photographs of food.
3) *Equivalence mode (true representational insight):* The animal or human associates pictures with objects, but knows that they are different, i.e. that the picture is a representation of the object. Therefore, the picture and object are processed differently.

Furthermore it is possible to categorize objects and pictures purely by characteristic visual 2D-features such as color or shape (*perceptual level* of picture-object recognition). Positive transfer between objects and pictures might therefore only be caused by recognition of a distinct feature without any comprehension of the object or the picture's representational nature. Finally, at the *associative level,* associations are formed between certain features or parts of an object and its picture. The subject recognizes the object depicted in the picture but has no understanding of the representational nature of the picture. (Grabner, 2010)

Even for humans picture-object recognition is not as easy as one would expect. Very young children find it difficult to recognize what is depicted in a picture because their visual apparatus is not fully developed yet (Slater et al. 1984) and the same holds true for cultures that are not accustomed to pictorial stimuli (Deregowski, 1989; Deregowski and Jahoda, 1975). There are two possible reasons for their problems: First, a two-dimensional representation of a three-dimensional object might be confusing to someone who has never

been confronted with pictures before. Second, there are certain technical shortcomings to pictures, such as resolution, chromatic replication, unnatural size/distance correspondence, and surface reflections (Deregowski, 2000).

If picture-object recognition can be this difficult for humans, then how much more problematic must it be for animals, given that they do not possess language to communicate what they perceive in a picture or to tell them what a picture represents? There are two main approaches to test whether animals recognize pictures as representations of real objects (Spetch et al., 2000). The first one is to show transfer of a learned response from an object to its picture and vice versa. For pigeons this has successfully been shown in many studies (e.g. Cabe, 1976; Cole and Honig, 1994; Looney and Cohen, 1974; Spetch and Friedman, 2006; Wilkie et al., 1989), but there have also been studies that showed no evidence of transfer (Dawkins et al., 1996; Dittrich et al., 2010; Lechelt and Spetch, 1997).

The second approach involves looking for appropriate behavioral responses such as courtship behavior or aggression towards pictures of biologically significant stimuli. Different animal species have been shown to respond spontaneously to pictures of conspecifics or food (chimpanzees: Boysen and Berntson, 1986, 1989; baboons and gorillas: Parron et al., 2008). These observations provide hints that some animals do recognize objects in pictures and speak against the independence mode of picture object recognition. However, they do not distinguish between confusion and equivalence mode, as pictures also evoke emotional responses in humans, even though they do not confuse pictures with real objects (Lang et al., 1998). In pigeons, aggressive (Looney and Cohen, 1974) and courtship behavior (Shimizu, 1998) towards photographs of conspecifics have been observed. Watanabe and colleagues (1993) showed that pigeons peck on pictures of food similarly as on real food. They prefer pecking on pictures of naturally colored corn compared to red or green corn, unless they were fed red corn before the experiment, which shows the importance of real-life experience with a

stimulus. Stephan and colleagues (2013) found that pigeons succeeded in discriminating pictures of familiar objects only, and they also showed the objects' relevance to the birds to influence their performance. Pigeons recognize new rotational views of familiar objects more easily than of unfamiliar objects (Watanabe, 1997a) and they show better transfer to pictures of familiar than of unfamiliar locations (Cole and Honig, 1994; Spetch et al., 1998; Wilkie et al., 1989). However, other studies showed no enhancing effect of familiarity on discrimination of pictures showing outdoor locations (Dawkins et al., 1996; Lechelt and Spetch, 1997) or even showed negative effects (Gray, 1987, cited in Dawkins et al., 1996).

Watanabe (1997b) showed that a certain type of brain lesion in pigeons affects the discrimination of food vs. non-food irrespective of whether the stimuli are presented in photographs or whether real 3D stimuli are used, but not the discrimination between pictures and real objects, which suggests different brain mechanisms being involved in these two tasks.

Another interesting question is whether animals are able to perceive depth information in pictures. One way to test this is via optical illusions, e.g. the Ponzo illusion or the Müller-Lyer illusion. Horses (Timney and Keil, 1996), monkeys (Bayne and Davis, 1983), and pigeons (Fujita et al., 1991, 1993; Nakamura et al., 2009) have shown to be perceptive to such illusions. As mentioned above, pigeons strongly rely on monocular depth cues due to the lateral placement of their eyes, and seem to be able to recognize these depth cues also in two-dimensional stimuli (Reid and Spetch, 1998).

1.2.2. Complementary information

Most studies concerning picture-object recognition in animals use pictures that contain some of the same perceptual information as the real objects, for example shape, color, or brightness (Loidolt et al., 2003). Therefore, correct discrimination of these pictures might not

show representational insight but rather stimulus generalization by means of visual cues that are present in both 2D and 3D representations of the objects *(perceptual* or *associative level).* Dasser (1987) showed that macaques could match photographs of different body parts of the same familiar conspecific, thereby providing evidence that her test subjects recognized other macaques on photographs. A study by Aust and Huber (2006) followed a similar logic. Pigeons were trained to respond to pictures showing incomplete human bodies and subsequently tested on pictures showing the previously missing parts. One group was trained with pictures of humans that never showed hands, and one group was trained with pictures that never contained heads. After an acquisition phase, pigeons were tested on photographs that showed hands for the "no-hands-group" and heads for the "no-heads-group". Both groups pecked more on previously missing parts of human bodies than on irrelevant pictures or pictures of skin patches. This showed that they recognized photographs of humans (and their parts) as representations of real humans (or parts of humans, respectively) because, other than on picture-object-transfer paradigms, the Complementary Information Procedure used by Aust and Huber did not involve the presentation of the same simple 2D-features in training and test stimuli. Instead, training and test stimuli contained complementary visual information. The results of that study were confirmed and extended in a follow up study (Aust and Huber, 2010), where the researchers could show that experience with humans was necessary for pigeons to classify the stimuli correctly, thus providing further evidence that pigeons can recognize humans in pictures.

In the present study I applied the Complementary Information Procedure, too, but used so-called Greebles – biologically irrelevant plastic figurines (see 2.3.) – as stimuli.

1.3. Rotational invariance

Rotational invariance describes the ability to identify an object or scene, even when it is presented under a previously unseen angle. Animal studies are especially interesting, because the animals' pre-experience with objects can be controlled, and they do not possess language to label objects.

There are two conflicting theories concerning rotational invariance. The first – known as Recognition-by-components (RBC) (Biederman and Gerhardstein, 1993, 1995) – describes viewpoint-independent object recognition. An object must fulfill three jointly sufficient criteria to be recognized. It must be composed of distinct parts (*geons*); a distinctive geon structural description (GSD) for each object must be formed; and this description must remain the same when the object is rotated, i.e. all parts must always be visible. Therefore an object should be recognized equally well from every viewpoint. Biederman (1987) and Biederman and Gerhardstein (1993) showed that rotation has little or no effect on object recognition for humans, while other studies found impairment in speed and accuracy (Diwadkar and McNamara, 1997; Edelman and Bülthoff, 1992; Hayward and Tarr, 1997; Rock and DiVita, 1987; Tarr, 1995; Tarr and Pinker, 1989).

Tarr and Pinker (1989) suggested an alternative theory, called multiple-views or viewpoint-dependent theory. Animals or humans form mental representations of specific viewpoints from which they previously encountered the object (Edelman and Bülthoff, 1992; Tarr and Bülthoff, 1995; Ullman, 1989) and then mentally transform a new image to see whether it matches a stored representation. These transformations have cognitive costs that are reflected in performance. According to this theory it should be easier to recognize novel views that lie within the range of views presented during discrimination training (interpolated) than views that lie beyond (extrapolated). Several studies have found these effects in pigeons and humans (Bülthoff and Edelman, 1992; Friedman et al., 2005; Hollard and Delius, 1982;

Peissig et al., 2000, 2002; Spetch and Friedman, 2003; Srinivas and Schwoebel, 1998; Wasserman et al., 1996) and even in bees (Dyer and Voung, 2008).

Experience with objects seems to affect viewpoint invariance for humans and animals (Edelman and Bülthoff, 1992; Tarr, 1995). Rock and DiVita (1987) found a lack of viewpoint invariance in humans if they had no previous experience with the presented objects. Similarly, Watanabe (1997a) found that his pigeons recognized new rotations of a feeder, which they encountered in their every-day lives, but not of a mug, and he found that exposure to wooden blocks had a positive effect on discrimination learning and recognition of unknown views of these blocks (Watanabe, 1999).

In conclusion, it is still not clear whether object recognition in pigeons and humans is viewpoint-dependent or not. It seems that the object's characteristics, number of training views, and real-life experience with the objects play an important role in whether or not they are recognized equally well from all angles.

1.4. Preliminary study

A preliminary study was conducted by Stephan and colleagues (subm., unpublished data) prior to the experiment described in the present thesis to investigate object recognition and representational insight in pigeons and humans using 2D and 3D stimuli. Nineteen pigeons were trained to discriminate between two objects (Greebles, see 2.3.), using either real objects, photographs of these objects on a computer screen, or holograms of the objects. After training, the pigeons were presented with objects, computer images, and holograms in the same contingencies, which showed the objects from previously unknown angles, i.e. views that were not shown during training, to see whether they would still be discriminated correctly. All three groups (object, hologram, and computer screen) succeeded in discriminating new views. The object and the computer screen group discriminated

interpolated views better than extrapolated views, while there was not enough data to test for these differences in the hologram group. Furthermore, all pigeons were tested in a complementary information task, using previously unseen parts of the objects as stimuli. The object and hologram groups succeeded in discriminating the new stimuli correctly, indicating that they did associate the stimuli used in training and test with the 3D objects installed in their aviary, while the computer screen group failed. One possible explanation for these differences might be that the pigeons trained with real objects and holograms lived in an aviary where the real objects were present at all times and could be viewed from all sides, while the pigeons trained on computer screens lived in the adjacent aviary and could see the objects only from a limited number of angles. Since previous studies have shown easier generalization to new views of familiar objects than of unfamiliar objects (Watanabe, 1997a; Wilkie et al., 1989) the present study was conducted as a follow-up study, using the same computer screen stimuli as the preliminary study, but testing pigeons that lived in the aviary where the objects were installed.

1.5. Aims

The main goal of this study was to expand our knowledge about picture-object recognition in pigeons. Pigeons were trained to discriminate two-dimensional, rotated views of biologically irrelevant stimuli on a computer screen, and it was subsequently tested whether this discrimination could be transferred to previously unseen views (rotational invariance). Additionally I looked at differences in performance on interpolated and extrapolated test views to find out whether the discrimination was viewpoint-dependent or -independent. A group of humans was tested on the same test to compare performance between two highly visual species and find possible differences or similarities. Furthermore, I tested whether direct visual contact to the real-life objects facilitates this discrimination via

comparing the results of this study to the previous study conducted by Stephan and colleagues (unpublished data).

Following the Complementary Information Procedure (CIP) by Aust and Huber (2006) I subsequently tested whether pigeons are able to correctly discriminate photographs of parts of the objects that were not included in training after having visual access to the complete real-life objects, which would be indicative of picture-object recognition at a level beyond mere feature discrimination. These results were again compared to the previous study to find a possible influence of the degree to which the pigeons were visually exposed to the 3D objects. If the pigeons in the present study performed better than the pigeons in the previous study this would indicate a positive influence of more direct visual access to the 3D objects. If not, the results of the previous study – better performance of pigeons trained with real objects and holograms than pigeons trained with computer images – were caused by the different stimulus types (2D vs. 3D).

II. METHODS

2.1. Subjects

Pigeons. Nine pigeons (*Columba livia*) of an Austrian breed called Strasser and of mixed sex were tested in this study. Three of those pigeons started training later than the rest due to the decease of two of the original pigeons employed for the study. During the experiment the pigeons were housed together in an outdoor aviary (300 x 120 x 170cm) that was equipped with perches and nesting boxes. They were kept at about 90% of their free-feeding weight. On testing days they only received food during the experimental sessions and some post-testing supplementary feeding, while on non-testing days they received extra rations of food. Water and grit were freely available. All birds had previously participated in visual discrimination tasks but had no prior experience with pecking keys. None of the birds had experience with the go/no-go procedure, which was used in this study (see procedure section).

Humans. The subject group consisted of 11 humans (5 male / 6 female, 21-30 years of age). None of the participating humans had any pre-experience with visual discrimination experiments. All of them had normal or corrected-to-normal vision.

2.2. Apparatus

Pigeons. The experiments were conducted in five wooden indoor chambers ("Skinner boxes"), whose front walls were replaced by 15inch PC monitors with a resolution of 1024 x 768 pixels. In front of each PC monitor, at a distance of 5cm, a transparent response key was installed (∅ 5cm), allowing pigeons to see and respond to the stimuli that were presented on the screen. In the floor of the box, right in front of the pecking key, there was a special feeder to administer the rewards. It consisted of an electric motor that lifted a piston with a

depression on top through a grain reservoir underneath the box. The piston was then lifted through a hole in the floor of the box so that the pigeon could pick up the grain. The Skinner boxes were connected to a computer and controlled by a specially designed software package (CognitionLab Light 1.9; © M. Steurer, 2008) (see Steurer et al., 2012 for details).

Humans. Humans were tested on a PC with a Microsoft operating system, using the same software that was used in the pigeon experiment (CognitionLab Light 1.9; © M. Steurer, 2008). Instead of pecking they had to click on the presented stimulus using a standard computer mouse. They were not reinforced other than by getting faster through the sessions by reacting correctly to the stimuli.

2.3. Stimuli

For this study I used photographs of two objects called "Greebles" as training and test stimuli. Greebles are "face-like" artificially created objects with a homogeneous surface and several protruding parts (e.g. "arms" or "trunk") (Fig.1). Greebles were first created by Scott Yu at Yale University and named by the psychologist Robert Abelson, and they were first used in Isabel Gauthier's dissertation to determine whether face recognition in humans is an exclusive mechanism or a general mechanism based on configural sensitivity, that can also be used to discriminate non-face stimuli (Gauthier and Tarr, 1997; James et al., 2005).

For this study two differently shaped Greebles (Greeble 1 and Greeble 2) were used (Fig.1). Both consisted of a "head" with three appendages and a "trunk" with either one (Greeble 2) or two (Greeble 1) appendages and thus varied in number of appendages. Protected by Plexiglas cylinders a three-dimensional plastic version of each Greeble was installed in the aviary where the pigeons were housed, so that the animals had the possibility to visually explore the Greebles from all angles for several weeks before the experiment was started. Greeble 1 was 6.04cm and Greeble 2 6.14cm in height. To give the human subject

group some pre-exposure to the three-dimensional Greebles prior to the experiment they spent about 1.5 hours in a room where the Greebles were placed inconspicuously, so that the participants had a chance to see them before they started the experiment without being aware of their relevance.

During experimental sessions the stimuli were presented with a wavelength of 540nm (which appears green to the human eye) on a black background (RGB 0,0,0) at the center of the screen. The stimuli used for training and in the first test were photographs of the trunk of Greeble 1 (120 pixels in height and 80 to 184 pixels in width, resulting in a 4.3cm x 2.8 to 6.5cm image on the screen, depending on the angle from which the photograph was taken) and photographs of the trunk of Greeble 2 (125 pixels in height and 106 to 168 pixels in width, resulting in a 4.4cm x 3.7 to 5.9cm image on the screen). The stimuli used for the second test were photographs of the head of Greeble 1 (about 57 pixels [2cm] in height and 94 to 116 pixels [3.3 to 4.1cm] in width), and photographs of the head of Greeble 2 (about 57 pixels [2cm] in height and 92 to 170 pixels [3.3 to 6.0cm] in width). In the third test the Greebles' heads were presented in different sizes, ranging from 20% to 180% of their original size (see table 1 for a list of all head sizes in pixels and centimeters) (see Appendix for all stimuli used in this study).

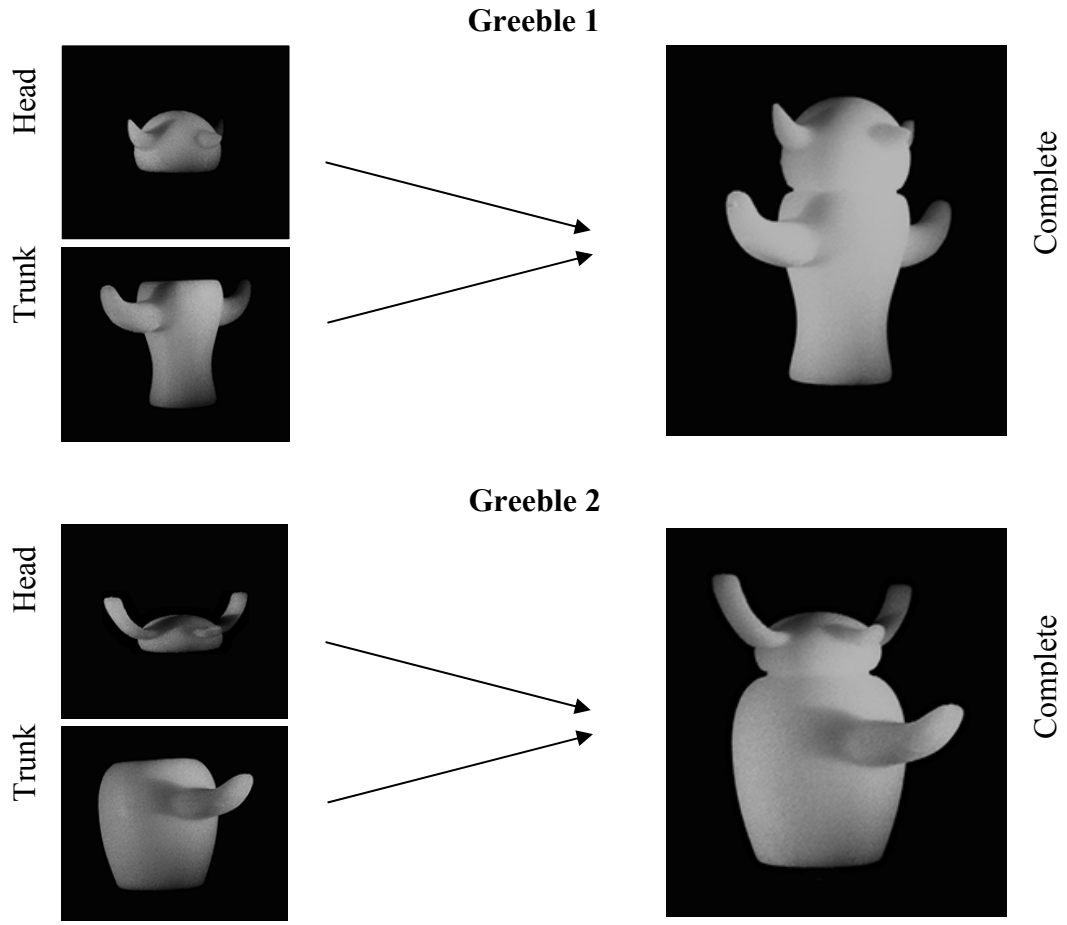


Fig.1: The two Greebles used in this study. On the left the trunks and heads are shown separately, while on the right the complete Greebles are shown. Note that they vary in size and shape of their trunks, heads, and appendages, and also in the number of appendages.

2.4. Procedure

Pigeons were trained and tested in a go/no-go procedure as described by Vaughan and Greene (1984). Only one stimulus was presented at a time and pigeons responded to it either by pecking on the pecking key or by withdrawing from pecking, while humans responded by clicking on the stimulus presented on a computer screen with a standard computer mouse. This made it possible to measure graded responses to stimuli. Pecks and clicks were counted for the first 15 seconds of stimulus presentation (presentation interval, PI), and the stimulus remained visible for another 1 to 15 seconds (variable interval, VI) if the response

requirement was accomplished, or longer if it was not accomplished. In case of a positive training stimulus the subjects had to peck (pigeons) or click (humans) at least ten times in total and two times per second after the presentation interval, which led to the disappearance of the stimulus after the variable interval and for pigeons to reinforcement in the form of five seconds food access. In case of a negative training stimulus the subjects had to withdraw from pecking or clicking for eight seconds after the presentation interval to make the stimulus disappear after the variable interval. No food was delivered in negative trials.

Test stimuli were presented for 15 seconds (PI), during which responses were recorded, and then another 1 to 15 seconds (VI). Unlike the training stimuli, test stimuli were of neutral contingency and therefore never reinforced. They disappeared after the VI, regardless of the test subject's responses. All pecks or clicks that were emitted between the 5th and the 15th second after the stimulus appeared entered analysis. The first five seconds of stimulus presentation were not used for analysis because the subjects often needed time to focus on the stimulus, for example because the pigeons often turned away from the screen and took a few seconds to turn back. Between trials there was a random inter-trial interval (ITI) of 15 to 40 seconds, and the start of each trial was accompanied by an acoustic signal (600Hz, 1sec) to draw attention to the stimulus.

Pretraining. Since the pigeons had not worked with pecking keys before they received a simple pre-training in the form of a standard autoshaping procedure before the actual training to familiarize them with the basic procedure. Humans received a brief verbal instruction in which they were introduced to the basic response requirements during the experiment. In particular, they were instructed to learn to distinguish positive from negative stimuli by trial and error, with positive stimuli disappearing upon continued clicking and negative stimuli disappearing upon withdrawal from clicking. They were not told how many positive and negative stimuli they would be presented with, which features characterized

positive and negative stimuli, and how often and for how long they had to click. However, they were told to click at least two times per second on a positive stimulus. Humans also received a short pre-training during which they had to learn to discriminate between six positive and six negative stimuli which were randomly chosen.

Discrimination training. Pigeons and humans were trained to discriminate between photographs of the two Greebles' trunks (Fig.2) (see Appendix for a list of all training stimuli). The photographs of the trunks of both Greebles were taken from a randomly assigned 0° view and then rotated clockwisely to 30°, 60°, 120°, 150°, 180°, 240°, and 250°, thus resulting in a total of 16 training stimuli (eight for Greeble 1 and eight for Greeble 2). The training stimuli were split into two groups – 0° to 120° and 150° to 250° – and each training session consisted of all stimuli from one group with each being presented four times, adding up to 32 trials per session – 16 positive and 16 negative ones. The trial sequences were pseudo-randomized, so that each session started and ended with a positive trial, and there were never more than three consecutive trials of the same contingency (negative or positive) in a row. The same sessions were used for pigeons and humans, but for humans inter-trial intervals were reduced from 15-40 to 2-5 seconds. Greeble 1 was assigned positive for four pigeons and six humans; Greeble 2 was positive for five pigeons and five humans.

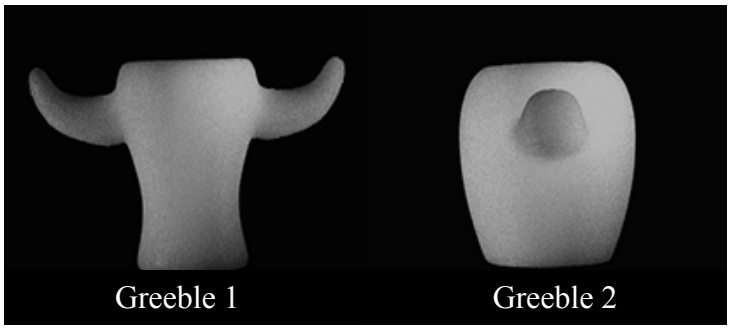


Fig.2: Trunks of Greeble 1 and Greeble 2, 0° view.

Rotational invariance test. After successfully mastering training, pigeons and humans were tested on a rotational invariance task to determine whether object recognition remained stable over different new test views. Test sessions involved the presentation of new views of the Greebles' trunks. These views were either interpolated (i.e. within the training range: 40°, 80°, 90°, 160°, 200°, and 210° rotation from a randomly chosen 0° view) or extrapolated (i.e. outside the training range: 270°, 280°, 300°, 320°, 330°, and 350° rotation) (see Appendix for a list of all test stimuli). Each session was pseudo-randomized, starting and ending with a rewarded trial and never having more than three unrewarded trials in a row. In each test session the positive and negative stimuli of only one new view were presented and repeated three times, so that each test session contained three positive and three negative test trials interspersed among 24 training trials (three positive and three negative training views repeated four times each), adding up to 30 trials per session in total. Each test view was used in two sessions with different training trials to get six repetitions for each positive and negative test view. In total the rotational invariance test consisted of 24 sessions that were presented in a different random order for each subject.

The sessions were the same for pigeons and humans, except for fewer repetitions (two instead of four) of training stimuli for humans, resulting in 18 trials per session. After finishing the experiment all human test subjects were asked to fill out a questionnaire, including questions about the perceived difficulty of the test and the stimuli (see Appendix).

Head-test. This test as well as the following were carried out only with the pigeons, because it was not possible to give the humans enough experience with the real Greebles. Both Greebles were installed in the outdoor aviary where the pigeons were housed from at least a few weeks (in case of the three birds employed later for the study) or months before starting training until they had finished all tests. For training and the rotational invariance task only photographs of the Greebles' trunks had been used. In the head-test I investigated if the

pigeons were able to transfer the discrimination of trunks to the (previously unseen) heads of the Greebles. If so, this would be evidence that they recognized the correspondence between the photographs of Greeble parts and the Greebles presented in the aviary.

The sessions were structured in the same way as in the rotational invariance task. They consisted of three repetitions of one positive and the corresponding negative test stimulus plus four repetitions of three different training stimuli. Again, each test view was used in two sessions, adding up to 16 sessions in total. The test stimuli were photographs of the Greebles' heads taken at the same angles as the training views of the trunks (0°, 30°, 60°, 120°, 150°, 180°, 240°, and 250°) (Fig.3) (see Appendix for a list of all test stimuli). The test trials were not reinforced and each session was pseudo-randomized, starting and ending with a rewarded trial and never having more than three unrewarded trials in a row.

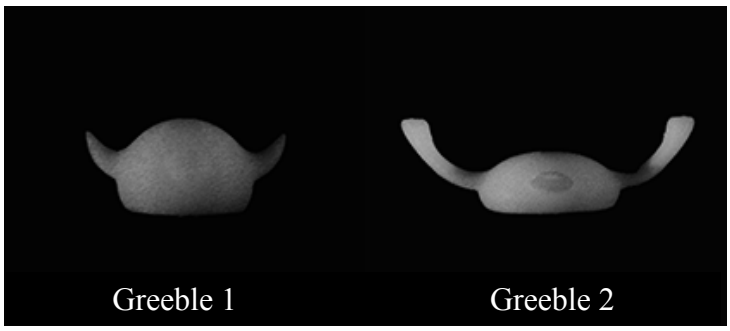


Fig.3: Heads of Greeble 1 and Greeble 2, 0° view.

Size-test. The head-test was repeated with stimuli of different sizes to determine whether stimulus size influenced the pigeons' responses (i.e. picture-object recognition). Three different photographs of each Greeble's head were used; taken from a 0°, 30°, and 90° angle. The stimuli were shown at 20%, 50%, 75%, 90%, 110%, 125%, 150%, and 180% of their original size (Table 1). Again, only one type of stimulus (i.e. positive and negative stimuli of one size of one angle) was used for each session and repeated three times,

interspersed among 24 trainings stimuli. Each test stimulus was used in two sessions, adding up to 48 sessions. Table 2 contains a list of all stimuli used in the present study.

Table 1: Sizes in pixels and centimeters of all test stimuli (heads) used in the Size-Test.

		Greeble 1		Greeble 2	
View	**Size**	**Pixels**	**Centimeters**	**Pixels**	**Centimeters**
0°	100%	116.00 x 54.00	4.09 x 1.90	170.00 x 55.00	6.00 x 1.94
	20%	23.20 x 10.80	0.82 x 0.38	34.00 x 11.00	1.20 x 0.39
	50%	58.00 x 27.00	2.05 x 0.95	85.00 x 27.50	3.00 x 0.97
	75%	87.00 x 40.50	3.07 x 1.43	127.50 x 41.25	4.50 x 1.46
	90%	104.40 x 48.60	3.68 x 1.71	153.00 x 49.50	5.40 x 1.75
	110%	127.60 x 59.40	4.50 x 2.09	187.00 x 60.50	6.60 x 2.13
	125%	145.00 x 67.50	5.11 x 2.38	212.50 x 68.75	7.50 x 2.43
	150%	174.00 x 81.00	6.14 x 2.85	255.00 x 82.50	9.00 x 2.91
	180%	208.80 x 97.20	7.36 x 3.42	306.00 x 99.00	10.80 x 3.49
30°	100%	106.00 x 54.00	3.74 x 1.90	155.00 x 60.00	5.47 x 2.12
	20%	21.20 x 10.80	0.75 x 0.38	31.00 x 12.00	1.09 x 0.42
	50%	53.00 x 27.00	1.87 x 0.95	77.50 x 30.00	2.74 x 1.06
	75%	79.50 x 40.50	2.81 x 1.43	116.25 x 45.00	4.10 x 1.59
	90%	95.40 x 48.60	3.37 x 1.71	139.50 x 54.00	4.92 x 1.91
	110%	116.60 x 59.40	4.11 x 2.09	170.50 x 66.00	6.02 x 2.33
	125%	132.50 x 67.50	4.68 x 2.38	193.75 x 75.00	6.84 x 2.65
	150%	159.00 x 81.00	5.61 x 2.85	232.50 x 90.00	8.21 x 3.18
	180%	190.80 x 97.20	6.73 x 3.42	279.00 x 108.00	9.85 x 3.82
90°	100%	94.00 x 54.00	3.32 x 1.90	92.00 x 56.00	3.25 x 1.98
	20%	18.80 x 10.80	0.66 x 0.38	18.40 x 11.20	0.65 x 0.40
	50%	47.00 x 27.00	1.66 x 0.95	46.00 x 28.00	1.63 x 0.99
	75%	70.50 x 40.50	2.49 x 1.43	69.00 x 42.00	2.44 x 1.49
	90%	84.60 x 48.60	2.99 x 1.71	82.80 x 50.40	2.93 x 1.78
	110%	103.40 x 59.40	3.65 x 2.09	101.20 x 61.60	3.58 x 2.18
	125%	117.50 x 67.50	4.15 x 2.38	115.00 x 70.00	4.06 x 2.48
	150%	141.00 x 81.00	4.98 x 2.85	138.00 x 84.00	4.88 x 2.97
	180%	169.20 x 97.20	5.98 x 3.42	165.60 x 100.80	5.85 x 3.56

Table 2: Summary of the stimuli used in the present study.

Procedure	Stimuli	
Training	trunks	0°, 30°, 60°, 120°, 150°, 180°, 240°, 250°
Rotational invariance test	trunks	interpolated: 40°, 80°, 90°, 160°, 200°, 210° extrapolated: 270°, 280°, 300°, 320°, 330°, 350°
Head-test	heads	0°, 30°, 60°, 120°, 150°, 180°, 240°, 250°
Size-test	heads 0° heads 30° heads 90°	20%, 50%, 75%, 90%, 110%, 125%, 150%, and 180% of original size 20%, 50%, 75%, 90%, 110%, 125%, 150%, and 180% of original size 20%, 50%, 75%, 90%, 110%, 125%, 150%, and 180% of original size

2.5. Data analysis

Discrimination training. Assessment of discrimination performance, i.e. differences in responses to positive and negative stimuli were based on Mann-Whitney U-tests for both pigeons and humans. For each session during discrimination training the number of pecks or clicks on the 16 positive and the 16 negative trials were compared. Discrimination training was successfully finished when there were significantly more responses to positive than to negative trials in four out of five consecutive sessions. To measure the performance on training stimuli the rho-value (ρ) was calculated. It describes the probability of the average rank of a positive stimulus being greater than the average rank of a negative stimulus (Herrnstein et al., 1976). A ρ-value of 1 indicates perfect discrimination, i.e. all positive stimuli have higher ranks than all negative stimuli. A ρ-value of 0.5 indicates chance performance, which means that the average ranks for positive and negative stimuli are the same. The sample size of six positive and six negative trials requires a ρ-value ≥ 0.861 to indicate significant discrimination ($\alpha = 0.05$).

Tests. For each test session the responses to positive and negative training trials were compared by means of a Mann-Whitney U-test. If a subject failed to correctly discriminate the training trials within a test session this session was repeated later in the test.

A sample size of six positive and six negative repetitions was used for individual test stimuli in each test, consisting of two sessions in which the test stimuli were repeated three times each. To compare the number of responses to stimuli over different sessions, the mean standardized response rate (MSRR) was calculated for each trial. It is described as the number of responses to one training or test stimulus in a session compared to the average number of responses to all positive and negative training stimuli of the same session. A mean standardized response rate above 1 indicates more responses to the respective stimulus than the average number of responses to positive and negative training stimuli in the same session, and a mean standardized response rate below 1 indicates fewer responses to the respective stimulus than the average number of responses to positive and negative training stimuli in the same session. MSRRs were used to make the subjects' response rates comparable across sessions and to provide relative values for comparing different individuals, compensating for inter- as well as intra-individual variations in response behavior. The mean standardized response rates of the six positive and six negative test stimuli were compared for each test view using the Mann-Whitney U-test to assess whether subjects significantly discriminated positive from negative stimuli within and across sessions.

Again, the ρ-value was calculated to assess performance. In the first test (rotational invariance test), 36 positive and 36 negative interpolated as well as 36 positive and 36 negative extrapolated stimuli were presented, therefore a ρ-value ≥ 0.635 was required to indicate significance. In the head-test I tested the pigeons with 48 positive and 48 negative test stimuli, and in the size-test I used 48 positive and 48 negative stimuli for each test view. Therefore, a ρ-value ≥ 0.616 was required.

To assess each subject's performance on training trials within a test six positive and six negative trials of each training view were randomly chosen from the last four sessions of the test. For each training view MSRRs of positive and negative trials were compared using the Mann-Whitney U-test. Furthermore, a ρ-value was calculated. To compare MSRRs and ρ-values between sessions and individuals the Mann-Whitney U-test was used. All data analysis was conducted using SPSS 14.0 and Microsoft Office Excel 2003 and 2007.

III. RESULTS

3.1. Discrimination training

Pigeons. After a brief pre-training phase pigeons were trained to discriminate photographs of the two Greebles' trunks in a go/no-go procedure. All nine pigeons reached the criterion of successful discrimination, which was defined as significant discrimination of positive and negative stimuli in four out of five consecutive sessions. The birds needed 84 training sessions on average (ranging from 16 to 187 sessions) to reach the discrimination criterion.

Humans. All 11 human test subjects succeeded at reaching the criterion. Eight of them discriminated the Greebles correctly from the first session on, and thus needed only four sessions to reach the criterion. Two humans needed five sessions and one needed seven sessions. Humans needed significantly fewer sessions than pigeons to successfully finish training (Mann-Whitney U-test; n1=9; n2=11; Z=-3.887; $p<0.0001$) (Fig.4), and humans trained on Greeble 1 needed fewer session than humans trained on Greeble 2 (Mann-Whitney U-test; n1=6; n2=5; Z=-2.098; $p=0.036$). There was no difference in performance between sexes (Mann-Whitney U-test; n1=5; n2=6; Z=-0.233; $p=0.816$).

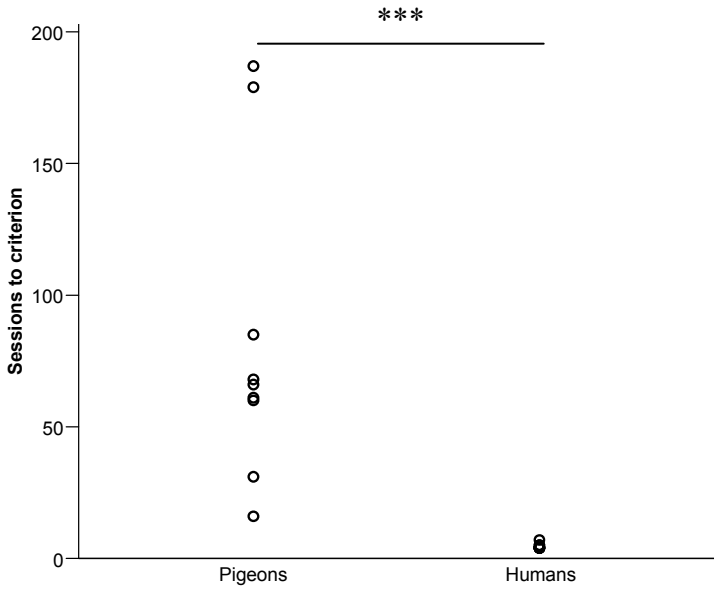


Fig.4: Number of sessions to criterion (correct discrimination of positive from negative stimuli in four out of five consecutive sessions) for pigeons and humans in the present study. * p≤ 0.05; ** p≤ 0.01; *** p≤ 0.001.

The seven pigeons in the preliminary study which did not have direct visual access to the three-dimensional Greebles in the aviary (i.e. the ones that were trained with pictures presented on a computer screen), needed 45 to 190 sessions to reach the criterion, with an average of 104 sessions. Although this was 20 sessions more than the average of 84 sessions for the pigeons in present study (i.e. the ones with more direct visual contact to the Greebles), there was no significant difference (Mann-Whitney U-test; n1=9; n2=7; Z=-0.953; p=0.340) (Fig.5). Like the pigeons in the present study, the subjects of the preliminary study showed great inter-individual differences in the number of trials that were needed to reach the acquisition criterion (see Appendix for detailed list).

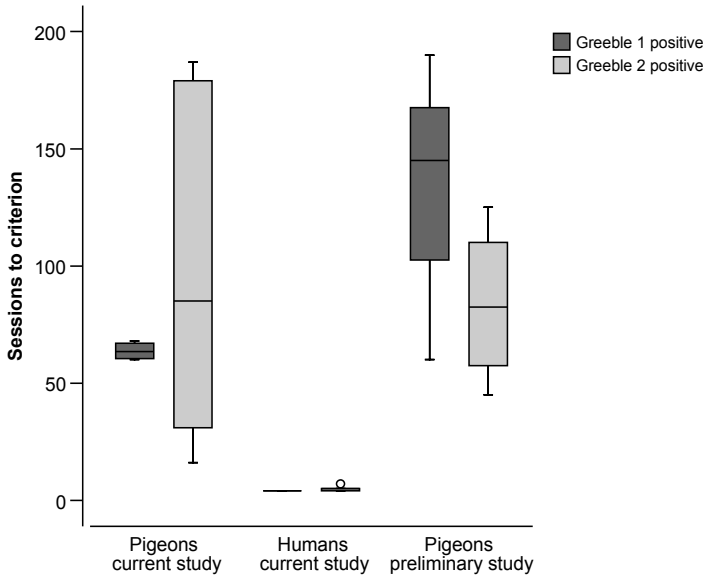


Fig.5: Number of sessions to criterion (correct discrimination of positive from negative stimuli in four out of five consecutive sessions) for pigeons and humans in the current study and for the pigeons in the preliminary study. Dark grey boxes represent the number of sessions to criterion for subjects trained to respond to Greeble 1; light grey boxes represent the number of sessions to criterion for subjects trained to respond to Greeble 2. The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers.

3.2. Rotational invariance test

In the rotational invariance test I wanted to investigate whether pigeons and humans are able to transfer their discrimination between photographs of Greebles to photographs of novel views of these Greebles (i.e. views which had not been shown during training). Therefore, pigeons and humans were tested on 12 unknown views of the Greebles' trunks, half of which were interpolated (40°, 80°, 90°, 160°, 200°, and 210°) and half of which were extrapolated (270°, 280°, 300°, 320°, 330°, and 350°) relative to the training stimuli. All subjects finished this test.

Both pigeons (Mann-Whitney U-test; n1=n2=108; Z=-8.845; $p<0.0001$) and humans (Mann-Whitney U-test; n1=n2=132; Z=-13.824; $p<0.0001$) discriminated positive and negative test stimuli correctly when interpolated and extrapolated stimuli were pooled (Fig.6

and 7). Pigeons discriminated positive and negative interpolated (Mann-Whitney U-test; n1=n2=54; Z=-7.957; p<0.0001) and positive and negative extrapolated (Mann-Whitney U-test; n1=n2=54; Z=-4.301; p<0.0001) test stimuli correctly, performed better on interpolated than on extrapolated test stimuli (Mann-Whitney U-test; n1=n2=54; Z=-2.402; p=0.016), and pecked significantly more on positive interpolated than on positive extrapolated stimuli (Mann-Whitney U-test; n1=n2=54; Z=-3.324; p=0.001). There were no such differences in performance between interpolated and extrapolated stimuli for humans (Mann-Whitney U-test; n1=n2=66; Z=-0.939; p=0.348), who also discriminated positive and negative interpolated (Mann-Whitney U-test; n1=n2=66; Z=-10.042; p<0.0001) and positive and negative extrapolated (Mann-Whitney U-test; n1=n2=66; Z=-9.500; p<0.0001) test stimuli correctly (Fig.8 and 9; Tables 3 and 4). Furthermore, pigeons (Mann-Whitney U-test; n1=54; n2=108; Z=-4.086; p<0.0001) and humans (Mann-Whitney U-test; n1=66; n2=132; Z=-3.038; p=0.002) performed better on known views (i.e. training views) than on new rotational views. Humans discriminated positive from negative new views significantly better than pigeons (Mann-Whitney U-test; n1=108; n2=132; Z=-10.710; p<0.0001) (Fig.6 and 7).

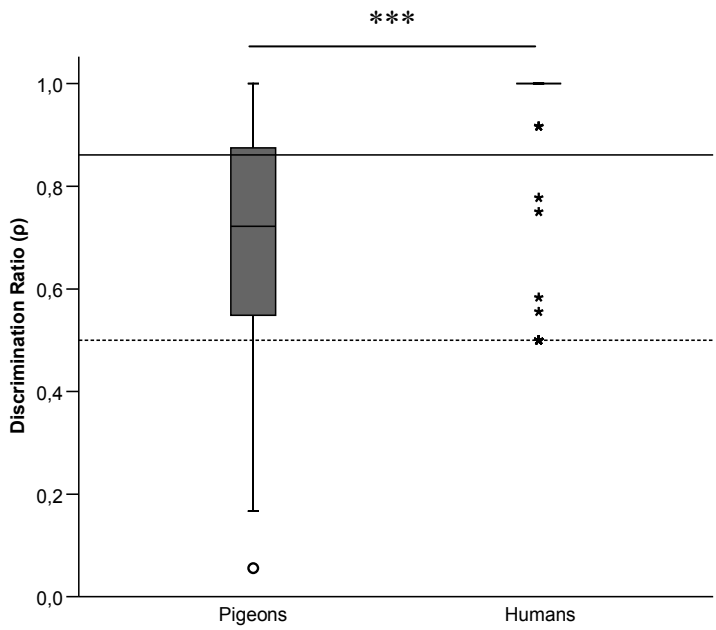


Fig.6: Performance of pigeons and humans in the rotational invariance test for all stimuli (interpolated and extrapolated pooled). The data includes the discrimination ratios (ρ-values) of each subject on the individual test stimuli. The bottom and top of each box indicate the first and the third quartile. The horizontal line within the box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers. Asterisks indicate values more than three times the height of the box. The dashed horizontal line indicates chance level (same ranks for positive and negative stimuli). The solid horizontal line indicates the limit of significance ($\rho \geq 0.8611$). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

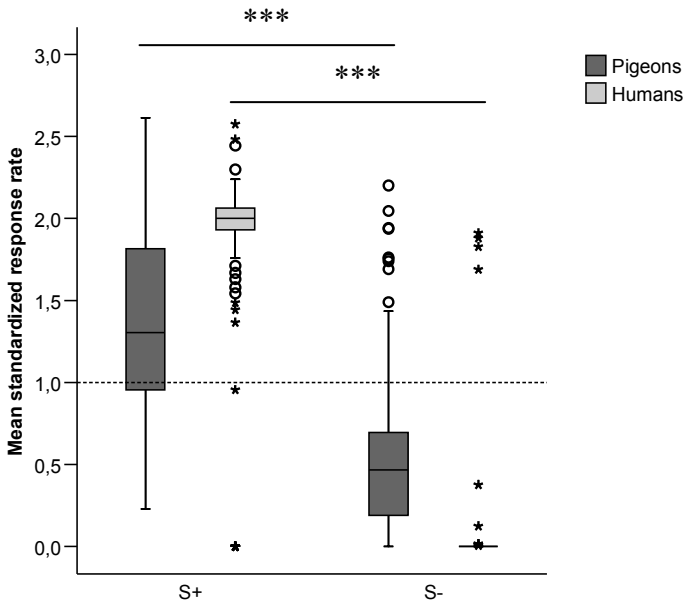


Fig.7: Mean standardized response rates to all positive (S+) and negative (S-) test stimuli (interpolated and extrapolated pooled) of pigeons and humans in the rotational invariance test. The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers. Asterisks indicate values more than three times the height of the box. The dashed horizontal line indicates chance level, i,e. the same number of responses to test stimuli as to positive and negative training stimuli. * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

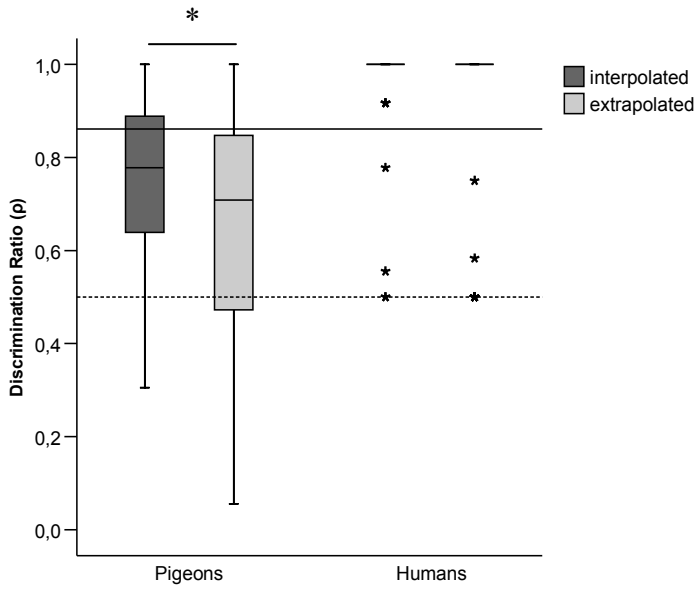


Fig.8: Performance of pigeons and humans on interpolated and extrapolated test stimuli in the rotational invariance test. Dark grey boxes represent the discrimination ratios (ρ-values) on every interpolated stimulus; light grey boxes represent the discrimination ratios (ρ-values) on every extrapolated stimulus. The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers. Asterisks indicate values more than three times the height of the box. The dashed horizontal line indicates chance level (same ranks for positive and negative stimuli). The solid horizontal line indicates the limit of significance ($\rho \geq 0.8611$). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

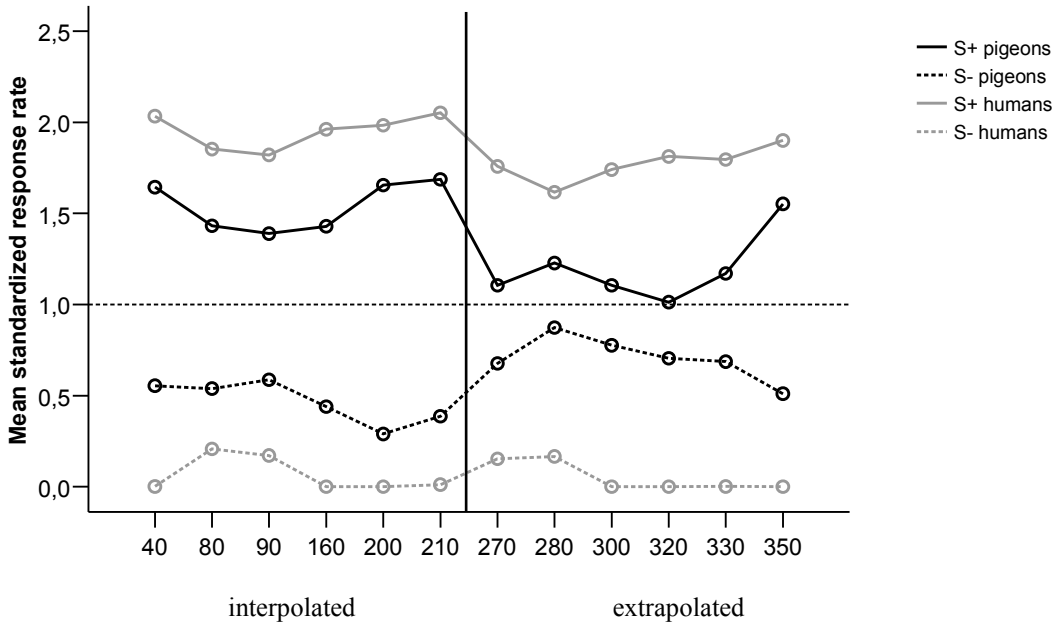


Fig.9: Mean standardized response rates to positive (S+) and negative (S-) stimuli of pigeons and humans in the rotational invariance test for each test view. The dashed horizontal line indicates chance level, i.e. the same number of responses to test stimuli as to positive and negative training stimuli. The vertical line separates interpolated from extrapolated test stimuli.

After finishing the test, each human participant filled out a short questionnaire (see Appendix). All test subjects reported the task to be easy. When asked how they discriminated positive from negative stimuli, five subjects stated that they used the overall form of the Greebles, four subjects used symmetry, and two used overall form and symmetry. When asked which parts or characteristics they used to discriminate the Greebles, five participants said that they compared the Greebles to familiar objects, e.g. “apple vs. cactus” or “one is shaped like a stylized bull head and the other like a vase”, five participants used the overall form of the Greebles’ trunks, e.g. “waist vs. belly”, and one participant wrote “either one or two arms, and when it has one arm its direction is relevant”.

Comparison of pigeons with and without real Greebles in their aviary (i.e. pigeons of the present study with pigeons of the preliminary study) revealed no difference in overall

performance (Mann-Whitney U-test; n1=108; n2=84; Z=-1.192; p=0.233). Furthermore, both groups performed better on interpolated than on extrapolated test stimuli (with Greebles in aviary: Mann-Whitney U-test; n1=n2=54; Z=-2.402; p=0.016; without Greebles in aviary: Mann-Whitney U-test; n1=n2=42; Z=-3.191; p=0.001) (Fig.10 and 11; Tables 3 and 4). In particular, pigeons in the present study responded more to positive interpolated than to positive extrapolated stimuli (Mann-Whitney U-test; n1=n2=54; Z=-3.324; p=0.001). Pigeons in the preliminary study responded more to negative extrapolated than to negative interpolated stimuli (Mann-Whitney U-test; n1=n2=42; Z=-2.827; p=0.005) (Fig.11). Like in the present study pigeons in the preliminary study performed better on known views (training trials) than on new views (Mann-Whitney U-test; n1=42; n2=84; Z=-2.538; p=0.011) (Fig.12).

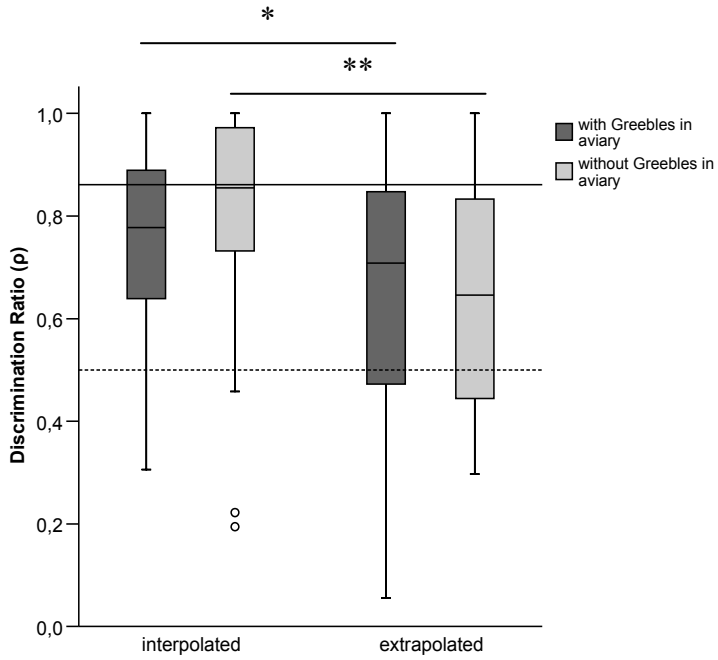


Fig.10: Performance of pigeons in the preliminary and pigeons in the present study (with and without real Greebles in their aviaries) on interpolated and extrapolated test stimuli in the rotational invariance test. Dark grey boxes represent the discrimination ratios (ρ-values) on every stimulus for pigeons in the present study; light grey boxes represent the discrimination ratios (ρ-values) on every stimulus for pigeons in the preliminary study. The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers. Asterisks indicate values more than three times the height of the box. The dashed horizontal line indicates chance level (same ranks for positive and negative stimuli). The solid horizontal line indicates the limit of significance ($\rho \geq 0.8611$). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

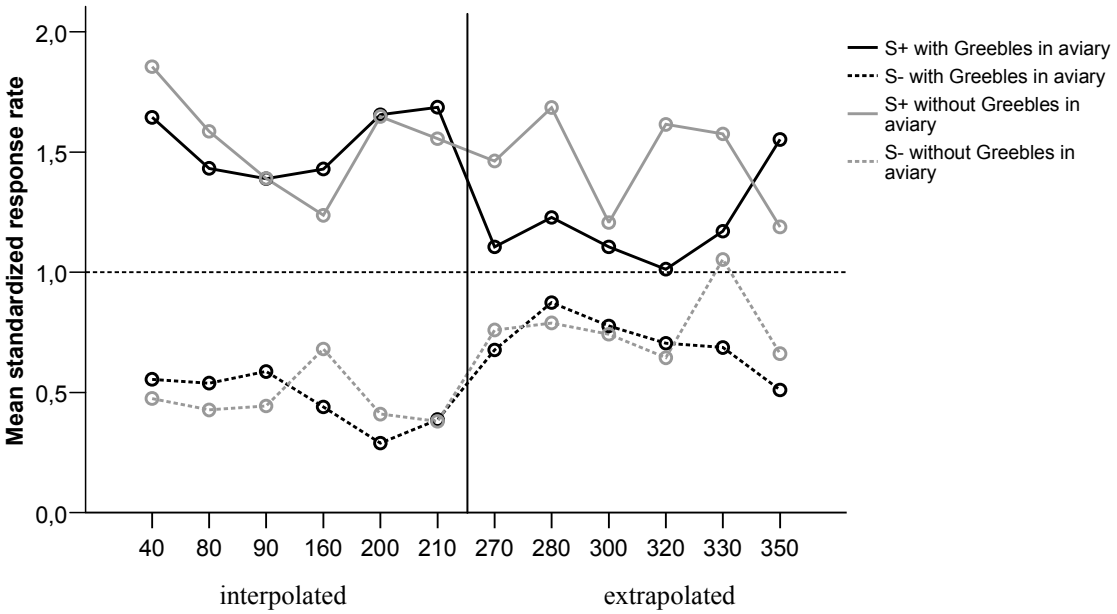


Fig.11: Mean standardized response rates to positive (S+) and negative (S-) stimuli of pigeons in the preliminary and pigeons in the present study (with and without real Greebles in their aviaries) on the rotational invariance test for each test view. The dashed horizontal line indicates chance level, i.e., the same number of responses to test stimuli as to positive and negative training stimuli. The vertical line separates interpolated from extrapolated test stimuli.

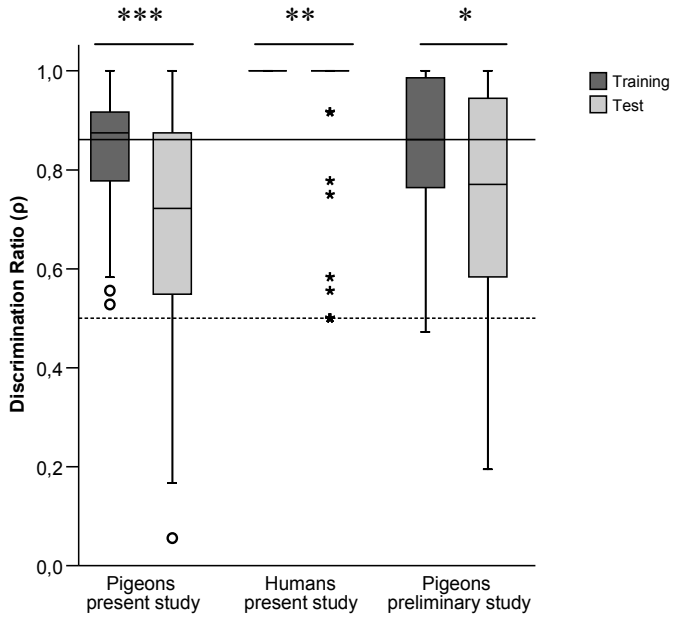


Fig.12: Comparison of rho-values for training and test stimuli in the rotational invariance test, shown for pigeons and humans in the present study and for pigeons in the preliminary study. Dark grey boxes represent the discrimination ratios (ρ-values) on every training stimulus; light grey boxes represent the discrimination ratios (ρ-values) on every test stimulus. The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers. Asterisks indicate values more than three times the height of the box. The dashed horizontal line indicates chance level (same ranks for positive and negative stimuli). The solid horizontal line indicates the limit of significance ($\rho \geq 0.8611$). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

Table 3: Rho-values for pigeons and humans for all interpolated test stimuli of the rotational invariance test.

	Subject	Exp. Group	Discrimination Ratio (ρ) all	40°	80°	90°	160°	200°	210°
Pigeons present study	Art	G1	**0.648**	0.667	0.667	0.431	0.528	**0.958**	0.611
	Electra	G1	**0.734**	0.583	0.542	0.569	**0.917**	0.667	**0.917**
	Lukas	G1	**0.760**	**1.000**	0.722	**0.917**	0.583	0.722	0.653
	Ron	G1	**0.689**	0.639	0.514	0.306	0.722	**1.000**	**0.875**
	Azurro	G2	**0.801**	0.833	0.847	0.778	0.667	**0.875**	0.833
	Hermine	G2	**0.828**	**0.875**	**1.000**	0.528	0.778	**0.917**	0.806
	Perdita	G2	**0.768**	0.792	0.611	**1.000**	0.472	0.778	**0.875**
	Steve	G2	**0.867**	0.847	**1.000**	**0.861**	0.736	0.694	**1.000**
	Vesper	G2	**0.779**	**0.889**	0.500	0.708	**0.917**	0.833	**1.000**
	Mean ±SD		**0.764 ±0.07**	0.792 ±0.14	0.711 ±0.20	0.678 ±0.23	0.702 ±0.16	0.827 ±0.12	0.841 ±0.14
Humans present study	H1	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H2	G1	**0.833**	**1.000**	0.500	0.500	**1.000**	**1.000**	**1.000**
	H3	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H4	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H5	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H6	G1	**0.986**	**1.000**	**1.000**	**0.917**	**1.000**	**1.000**	**1.000**
	H7	G2	**0.986**	**0.917**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H8	G2	**0.863**	**1.000**	0.778	0.556	**1.000**	**1.000**	**1.000**
	H9	G2	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H10	G2	**0.975**	**1.000**	**0.917**	**1.000**	**1.000**	**1.000**	**1.000**
	H11	G2	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	Mean ±SD		**0.968 ±0.06**	**0.993 ±0.03**	**0.927 ±0.16**	**0.907 ±0.19**	**1.000 ±0.00**	**1.000 ±0.00**	**1.000 ±0.00**
Pigeons preliminary study	Franz	G1		0.806	0.611	**0.861**	0.806	0.778	**0.944**
	Klara	G1		**1.000**	**1.000**	0.222	0.556	0.778	0.750
	Ferdinand	G1		**1.000**	**1.000**	**1.000**	0.639	**1.000**	**0.861**
	Cordula	G2		0.764	**0.861**	0.732	0.750	0.722	**0.859**
	Josef	G2		**0.850**	0.806	0.750	0.583	**0.972**	1.000
	Birgit	G2		**0.972**	**0.889**	0.458	0.194	**0.944**	0.667
	Meggie	G2		**0.944**	**1.000**	**0.972**	0.667	**1.000**	**1.000**
	Mean ±SD			**0.905 ±0.10**	**0.881 ±0.14**	0.714 ±0.28	0.599 ±0.20	**0.885 ±0.12**	**0.869 ±0.13**

Note: Values ≥ 0.635 for all interpolated stimuli irrespective of viewing angle ("all") and values ≥ 0.861 for individual test views indicate significant discrimination of positive and negative stimuli (sigificant values in bold typeface). Individuals in experimental group G1 were trained to respond to Greeble 1, individuals in experimental group G2 were trained to respond to Greeble 2. Empty cells mean that the respective data are missing.

Table 4: Rho-values for pigeons and humans for all extrapolated test stimuli of the rotational invariance test.

	Subject	Exp. Group	Discrimination Ratio (ρ) all	270°	280°	300°	320°	330°	350°
Pigeons present study	Art	G1	**0.806**	**1.000**	0.542	**0.917**	0.833	**0.972**	0.361
	Electra	G1	0.441	0.306	0.167	0.194	0.569	0.528	0.722
	Lukas	G1	0.465	0.319	0.472	0.056	0.319	0.500	**1.000**
	Ron	G1	0.465	0.222	0.250	0.472	0.236	0.333	**0.875**
	Azurro	G2	**0.702**	0.333	0.722	0.736	0.778	0.806	0.722
	Hermine	G2	**0.711**	0.792	0.556	0.583	0.722	0.708	**0.861**
	Perdita	G2	**0.677**	0.750	0.375	0.708	**0.944**	0.653	0.778
	Steve	G2	**0.866**	**0.861**	**1.000**	**0.861**	0.583	**0.972**	**0.944**
	Vesper	G2	**0.712**	**1.000**	0.833	0.847	0.556	0.556	0.542
	Mean ±SD		**0.649 ±0.16**	0.620 ±0.32	0.546 ±0.27	0.597 ±0.30	0.616 ±0.23	0.670 ±0.22	0.756 ±0.20
Humans present study	H1	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H2	G1	**0.833**	0.500	0.500	**1.000**	**1.000**	**1.000**	**1.000**
	H3	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H4	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H5	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H6	G1	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H7	G2	0.542	0.750	0.500	0.500	0.500	0.500	0.500
	H8	G2	**0.856**	0.583	0.500	**1.000**	**1.000**	**1.000**	**1.000**
	H9	G2	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H10	G2	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	H11	G2	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
	Mean ±SD		**0.930 ±0.14**	**0.894 ±0.19**	**0.864 ±0.23**	**0.955 ±0.15**	**0.955 ±0.15**	**0.955 ±0.15**	**0.955 ±0.15**
Pigeons preliminary study	Franz	G1		0.611	0.306	**0.944**	0.444	0.431	0.417
	Klara	G1		0.625	0.542	0.417	0.486	0.500	0.611
	Ferdinand	G1		0.583	0.583	0.600	0.694	0.417	**0.833**
	Cordula	G2		0.750	0.778	0.792	0.797	0.359	0.297
	Josef	G2		0.806	**1.000**	**0.889**	0.750	0.528	0.681
	Birgit	G2		**0.929**	**0.847**	0.361	0.417	**1.000**	0.319
	Meggie	G2		**1.000**	**1.000**	**1.000**	0.750	0.667	**0.889**
	Mean ±SD			0.758 ±0.16	0.722 ±0.26	0.715 ±0.26	0.620 ±0.16	0.557 ±0.22	0.578 ±0.24

Note: Values ≥ 0.635 for all interpolated stimuli irrespective of viewing angle ("all") and values ≥ 0.861 for individual test views indicate significant discrimination of positive and negative stimuli (sigificant values in bold typeface). Individuals in experimental group G1 were trained to respond to Greeble 1, individuals in experimental group G2 were trained to respond to Greeble 2. Empty cells mean that the respective data are missing.

3.3. Head-test

After finishing the rotational invariance task the pigeons were subjected to a complementary information test. Up to that point they had only seen photographs of the Greebles' "trunks" during the visual discrimination experiments, although they were housed with the complete real Greebles (including "trunks" but also "heads") in their aviary. In this test they were presented with photographs of different views of the Greebles' heads to see whether they could associate the heads with the corresponding trunks, which they had previously seen during training.

Three of the nine participating pigeons did not respond to any of the test stimuli and had thus to be excluded from further analysis. For the remaining six pigeons some stimuli had to be excluded from analysis because the subject did not respond to sufficient test trials. Of the six pigeons which finished the test, one discriminated the heads correctly (Mann-Whitney U-test; $n1=n2=48$; $Z=-2.002$; $p=0.045$) and one responded significantly more to pictures of the negative head than to pictures of the positive head (Mann-Whitney U-test; $n1=n2=48$; $Z=-2.596$; $p=0.009$) when all test views were pooled. The other four pigeons did not show significant differences in responses to positive and negative stimuli, neither when all test views were pooled nor for any single test view (Table 5). Pigeons performed better on training than on test views (Mann-Whitney U-test; $n1=36$; $n2=43$; $Z=-7.024$; $p<0.0001$) (Fig.13).

In the preliminary study six pigeons participated in the head-test. One of them discriminated the Greebles' heads correctly ($p<0.0001$), and one pigeon was excluded because it did not respond to the test stimuli at all (Table 5). There was no difference in the performance of pigeons with and without direct exposure to the Greebles (Mann-Whitney U-test; $n1=43$; $n2=48$; $Z=-0.875$; $p=0.381$). Like in the present study pigeons in the preliminary

study performed better on training views than on test views (Mann-Whitney U-test; n1=n2=48; Z=-6.597; p<0.0001) (Fig.13).

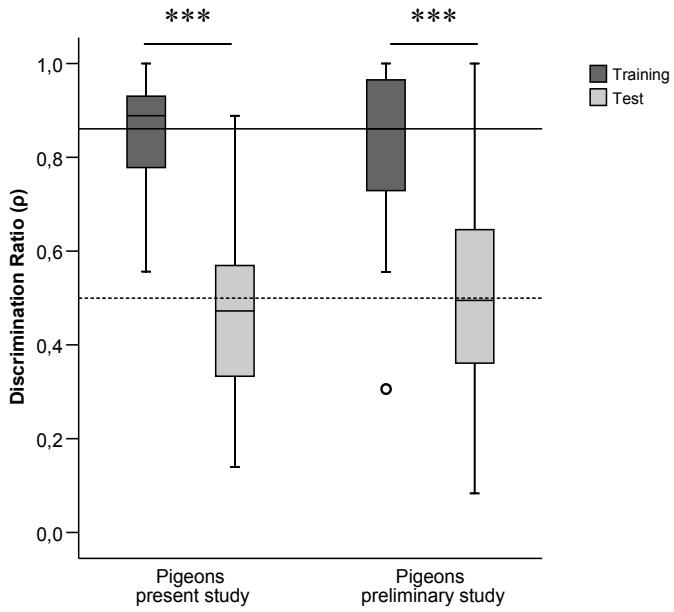


Fig.13: Comparison of rho-values for training and test stimuli in the head-test, shown for pigeons in the present study and for pigeons in the preliminary study. Dark grey boxes represent the discrimination ratios (ρ-values) on every training stimulus; light grey boxes represent the discrimination ratios (ρ-values) on every test stimulus. The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers. The dashed horizontal line indicates chance level (same ranks for positive and negative stimuli). The solid horizontal line indicates the limit of significance ($\rho \geq 0.8611$). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

Table 5: Rho-values for all test stimuli of the head-test.

	Subject	Exp. Group	Discrimination Ratio (ρ) all	0°	30°	60°	120°	150°	180°	240°	250°
Present study	Art	G1	**0.617**	0.167	**0.889**	0.556	0.514	0.833	0.681	0.611	0.472
	Electra	G1	0.487	0.194	0.597	0.333		0.764	0.556	0.444	
	Lukas	G1	0.449	0.514	0.139	0.528	0.500	0.611	0.569	0.514	0.333
	Ron	G1	0.415	0.139	0.556	0.569	0.361	0.361	0.417	0.444	0.403
	Azurro	G2	0.433	0.597	0.417		0.583	0.250	0.556	0.250	0.333
	Vesper	G2	***0.367***	0.333	0.806	0.264	0.444	0.389			0.222
	Mean ±SD		0.461 ±0.09	0.324 ±0.19	0.567 ±0.27	0.450 ±0.14	0.480 ±0.08	0.535 ±0.24	0.556 ±0.09	0.453 ±0.13	0.353 ±0.09
Preliminary study	Franz	G1		0.458	0.694	0.514	0.472	0.556	0.556	0.556	0.389
	Klara	G1		0.672	0.523	0.477	0.414	0.639	0.361	0.361	0.375
	Ferdinand	G1		0.708	0.750	0.806	0.250	**1.000**	**0.861**	**0.944**	0.250
	Josef	G2		0.458	0.083	0.514	0.653	0.583	0.361	0.361	**0.861**
	Birgit	G2		0.333	0.708	0.722	0.250	0.556	0.389	0.278	0.625
	Meggie	G2		0.306	0.306	0.542	0.306	0.278	0.569	0.417	0.444
	Mean ±SD			0.489 ±0.17	0.511 ±0.27	0.596 ±0.13	0.391 ±0.16	0.602 ±0.23	0.516 ±0.19	0.486 ±0.24	0.491 ±0.22

Note: For all stimuli irrespective of viewing angle ("all") values ≥ 0.616 indicate correct discrimination of positive and negative stimuli (significant values in bold), and values ≤ 0.384 indicate significantly higher ranks for negative than for positive stimuli (significant values in Italics). Values ≥ 0.861 for individual test views indicate significant discrimination of positive and negative stimuli (significant values in bold). Missing values indicate that the individual did not respond in a sufficient number of test trials to allow for data analysis or that the data is missing. Individuals in experimental group G1 were trained to respond to Greeble 1, individuals in experimental group G2 were trained to respond to Greeble 2. Empty cells mean that the respective data are missing.

3.4. Size-test

To further investigate the pigeons' ability (and the limits of the latter) to associate photographs with their real-life counterparts they were tested with a complementary information procedure with differently sized photographs of the Greebles' heads, shown at 0°, 30°, and 90°. Five pigeons participated in this test. Four of them finished it, while one pigeon finished only the sessions with the 0° and 90° test stimuli. Again, some test views had to be excluded from analysis for individual pigeons because they did not respond to them. The size-test was not performed in the preliminary study.

Analysis of all test stimuli pooled (all pigeons and all views) revealed no significant difference in responses to positive and negative stimuli (Mann-Whitney U-test; n1=n2=112; Z=-0.130; p=0.897). Analysis of the data of all pigeons pooled but with separate assessment of performance with the individual views showed that they responded significantly more to positive than to negative test stimuli for the 30° view (Mann-Whitney U-test; n1=n2=32; Z=-3.732; p<0.0001) and significantly less to positive than to negative test stimuli for the 0° view (Mann-Whitney U-test; n1=n2=40; Z=-2.347; p=0.019). There was no difference for the 90° view (Mann-Whitney U-test; n1=n2=40; Z=-1.602; p=0.109) (Fig.14; Table 6). When data of all pigeons were pooled no differences in response rates to positive and negative stimuli for any individual stimulus size were revealed (Fig.15). Performance was better on training views than on test views (Mann-Whitney U-test; n1=30; n2=61; Z=-5.753; p<0.0001) (Fig.16).

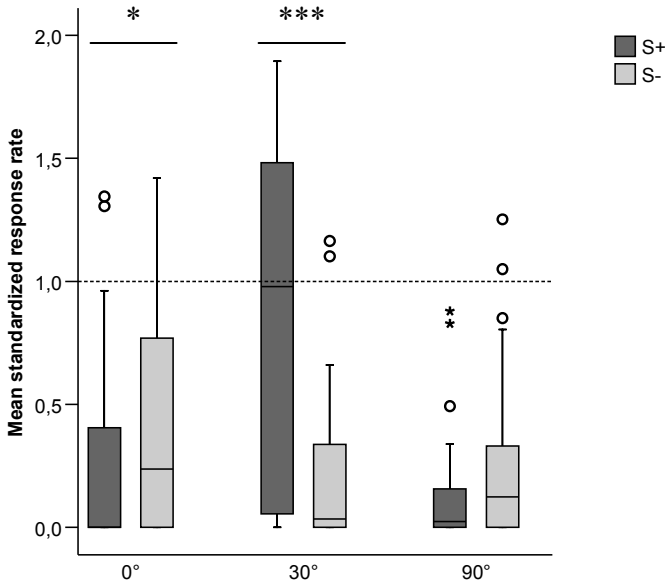


Fig.14: Mean standardized response rates to positive (S+) and negative (S-) stimuli in the size-test, shown separately for each view (0°, 30°, and 90°). The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers. Asterisks indicate values more than three times the height of the box. The dashed horizontal line indicates chance level, i.e. the same number of responses to test stimuli as to positive and negative training stimuli. * p≤ 0.05; ** p≤ 0.01; *** p≤ 0.001.

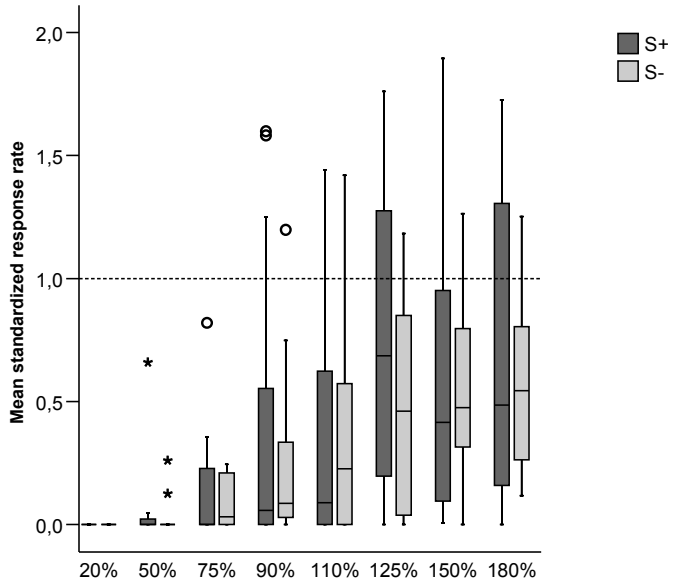


Fig.15: Mean standardized response rates to positive (S+) and negative (S-) stimuli in the size-test, pooled for each size (20% to 180% of original size). Dark grey boxes represent the numbers of responses to positive stimuli (S+); light grey boxes represent the the numbers of responses to negative stimuli (S-). The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. Circles indicate outliers that do not fall in the whiskers. Asterisks indicate values more than three times the height of the box. The dashed horizontal line indicates chance level, i.e. the same number of responses to test stimuli as to positive and negative training stimuli.

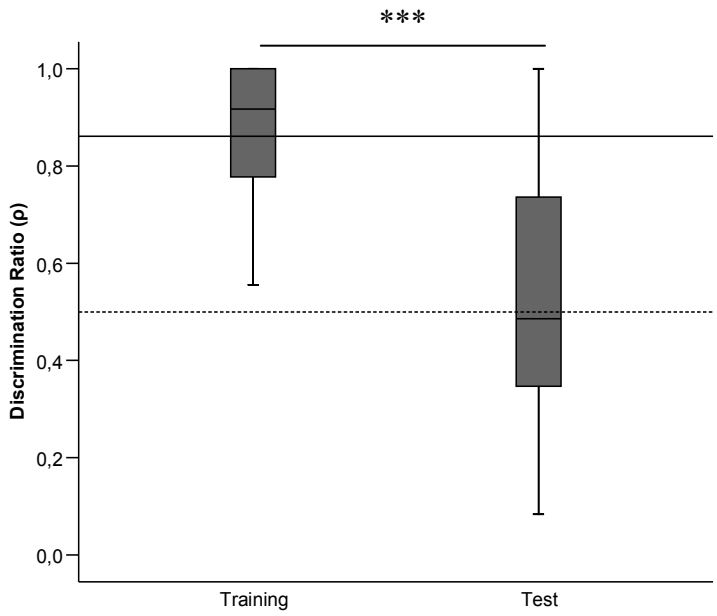


Fig.16: Comparison of rho-values for training and all test stimuli pooled for all pigeons in the size-test. The bottom and top of each box indicate the first and the third quartile. The horizontal line within each box represents the median. Whiskers indicate values that are 1.5 times the height of the box. The dashed horizontal line indicates chance level (same ranks for positive and negative stimuli). The solid horizontal line indicates the limit of significance ($\rho \geq 0.8611$). * $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$.

Table 6: Rho-values for all test stimuli of the size-test.

	Subject	Exp. Group	Discrimination Ratio (ρ) all	20%	50%	75%	90%	110%	125%	150%	180%
0°	Art	G1	0.493				0.556	0.222	0.361	0.444	0.583
	Electra	G1	0.388				0.167	0.083	0.694	0.361	0.583
	Lukas	G1	0.397					0.167		0.292	0.444
	Ron	G1	0.400				0.250	0.236	0.542	0.139	0.472
	Vesper	G2	0.469						0.375		0.375
	Mean		0.429				0.324	0.177	0.493	0.309	0.491
	±SD		±0.05				±0.20	±0.07	±0.16	±0.13	±0.09
30°	Art	G1	**0.664**			**0.861**	**1.000**	**0.875**	**0.861**	0.639	0.222
	Electra	G1	**0.747**				**0.917**	**0.917**	**0.903**	**1.000**	0.736
	Lukas	G1	**0.664**			0.750	**0.903**	0.792	**0.972**	**0.944**	0.736
	Ron	G1	0.590				0.514	0.625	0.806	0.639	0.750
	Vesper	G2	-	-	-	-	-	-	-	-	-
	Mean		0.666			0.806	0.834	0.802	**0.886**	0.806	0.611
	±SD		±0.06			±0.08	±0.22	±0.13	**±0.07**	±0.19	±0.26
90°	Art	G1	0.471			0.500	0.444	0.292	0.319	0.500	0.486
	Electra	G1	0.432				0.444	0.361		0.319	
	Lukas	G1	0.431						0.250	0.472	0.250
	Ron	G1	0.442						0.417	0.389	0.319
	Vesper	G2	0.485				0.583	0.417		0.611	0.347
	Mean		0.452				0.490	0.357	0.329	0.458	0.351
	±SD		±0.02			0.500	±0.08	±0.06	±0.08	±0.11	±0.10

Note: Values ≥ 0.616 for all stimuli irrespective of viewing angle and values ≥ 0.861 for individual test views indicate significant discrimination of positive and negative stimuli (significant values in bold). Missing values indicate that the individual did not respond in a sufficient number of test trials to allow for data analysis. Individuals in experimental group G1 were trained to respond to Greeble 1, individuals in experimental group G2 were trained to respond to Greeble 2.

IV. DISCUSSION

4.1. Discrimination training

As expected, humans were very fast in learning to discriminate positive from negative stimuli, and all of them reported the task to be easy. Pigeons needed much longer, and there were great differences between individual pigeons, with some reaching the criterion within a few weeks and others needing many months of training. Although there were no significant differences between pigeons trained on Greeble 1 and Greeble 2, there were bigger inter-individual differences in learning speed for pigeons being trained on Greeble 2. A similar effect was found for humans, with all humans trained on Greeble 1 discriminating the Greebles correctly from the first session on, and more than half of the humans being trained on Greeble 2 needing more than four sessions. It remains unclear whether these differences were due to the Greebles' features or inter-individual differences between test subjects. There was no difference in acquisition speed between the pigeons in this study and the pigeons in the preliminary study, which had only limited visual contact to the 3D Greebles. Therefore, 360° visual contact with objects did not facilitate discrimination between two-dimensional representations of these objects. However, the photographs used for training only contained the Greebles' trunks, so it is possible that the pigeons did not recognize them as parts of the real objects they were used to seeing. This question was addressed in the complementary information test.

4.2. Rotational invariance test

The aim of this test was to investigate whether pigeons can recognize unfamiliar rotated two-dimensional views of objects and to compare their performance with that of humans. We could show that both pigeons and humans were able to discriminate the new views correctly. Humans were significantly better than pigeons, and they reported to find the task very easy. Most of them used the shape of the Greebles' trunks and the number of appendages to discriminate the Greebles, or they compared them to familiar objects such as apples or vases. Ten of the 11 humans learned to respond correctly despite rotation of the photographs. One human developed a different strategy of responding to the positive Greeble (in this case Greeble 2). Namely, the subject responded only when the Greeble's arm was pointing to the right but did not respond when it was pointing to the left. Although the participants were not told when they had finished training and started the test phase, this participant reported orally to have noticed that at some point new stimuli appeared, and that he/she thus treated the latter differently than the ones known from training. In other words, this participant made a distinction between positive training and test stimuli instead of generalizing from the former to the latter, which, of course, resulted in poor transfer performance overall. There were also other participants who reported to have noticed the change from training to test phase, but all of those solved the task correctly (i.e. generalized from training views to novel ones).

All pigeons discriminated interpolated test stimuli correctly, but three out of nine did not discriminate extrapolated test stimuli correctly. The same holds true for the pigeons in the preliminary study, which also performed significantly better on interpolated than on extrapolated test stimuli. As figure 11 shows there were two reasons for this result: in the current study pigeons pecked significantly more on positive interpolated test trials than on positive extrapolated test trials, indicating a more decisive response to positive interpolated

stimuli and a more cautious response to positive extrapolated stimuli. Furthermore, in the preliminary study pigeons pecked significantly more on negative extrapolated test stimuli than on negative interpolated test stimuli, which shows less inhibition on negative extrapolated test stimuli. This pattern is seen in both groups, even though the current study did not yield significant differences in response rates for negative test stimuli. A bigger sample size might be necessary to see whether this pattern can reliably be found in both groups. This difference in performance on interpolated and extrapolated test stimuli supports the viewpoint-dependent theory of rotational invariance, meaning that to discriminate new stimuli the pigeons used a mental representation of known stimuli and compared them to the test stimuli, which made it easier for them to discriminate new views of the stimuli that lay between the training views. This has previously been shown for pigeons in other studies (e.g. Friedman et al., 2005; Spetch and Friedman, 2003; Srinivas and Schwoebel, 1998). I could not show this effect for humans, who also reported to have discriminated the Greebles by the shape of their bodies and the number of arms, which would point to a viewpoint-independent approach of object recognition and to an account in terms of geons. Friedman and colleagues (2005) showed that humans benefit from the presence of one distinct diagnostic component (geon), but pigeons do not, which fits well with my results. Another explanation for the human participants' viewpoint-independent discrimination might be that the Greebles were very easily discriminable to humans. Hayward and Williams (2000) showed that viewpoint dependence increases with increasing difficulty of the task.

There was no difference in performance of pigeons with and without direct exposure to the Greebles. This can be explained in two ways: either it was enough to see the Greebles only from a limited number of angles for the pigeons in the preliminary study to form mental representations of them, so that both groups used mental representations to discriminate new

views, or both groups did not form mental representations but discriminated the Greebles by using 2D features in the photographs.

4.3. Head-test

One of the six tested pigeons distinguished the photographs of the heads correctly, while one other pigeon pecked significantly more on the negative stimuli. Interestingly, although they were originally trained to respond to different Greebles, both actually preferred the same head – which was positive for one pigeon, and negative for the other. This suggests a preference for item-specific features in the picture of this head. Four pigeons did not show any preference, so that overall there was no indication for picture-object recognition in these pigeons. Three test subjects did not respond to the stimuli sufficiently to allow for analyzing the data. It is important to note that these three pigeons did, however, respond correctly to the training trials during the test. It can therefore be concluded that they refused to respond to the test stimuli not because of a general lack of motivation but because the test trials were not reinforced, i.e. the stimulus disappeared after a certain amount of time, irrespective of whether or not the pigeons pecked. Alternatively or in addition, they may have refused to respond to the stimuli because of their unfamiliar appearance (Aust and Steurer, 2013; Clement and Zentall, 2003).

Comparing the present to the preliminary study we could not find any difference in performance that may have been due to direct (and full) versus indirect (and limited) exposure to the 3D Greebles. Like in training and in the rotational invariance test, direct visual contact to the Greebles did not improve performance. In the preliminary study there was also one pigeon which discriminated the heads correctly and thus seemed to show indication of representational insight. The fact that in each group one pigeon passed the test suggests that at least for those two birds it was not necessary to see the 3D objects from all angles, but that a

limited number of viewing angles was sufficient. However, the fact that only two of all 12 birds in the preliminary and the present study succeeded in discriminating the pictures of the Greebles' heads correctly and one bird even discriminated them significantly "wrong", while the other nine showed no preference or did not respond to the heads at all offers no encouragement for the view that any of the pigeons in either study may indeed have recognized the correspondence between the photographs and their 3D-referents in the aviary. Because the pigeons tested with 3D objects and holograms in the preliminary study succeeded (Stephan et al., subm.) it seems likely that it is easier for pigeons to generalize from one three-dimensional stimulus to another (recognition of an object in different contexts), while it is more difficult for them to generalize from a three-dimensional stimulus to a two-dimensional stimulus (picture-object recognition). There are at least two possible reasons for this result: First, while depth information is available in real objects or holograms, information about the third dimension is lost when photographs are used as stimuli. Second, pictures on a computer screen might look very similar to the real objects for humans, but it is not clear what a pigeon perceives when looking at a screen. For sure, to a pigeon, a computer image will appear very different from the real object.

4.4. Size-test

When testing with differently sized stimuli I obtained inconsistent results, as pigeons' performance seemed to depend on the angle at which the Greebles were presented. Most pigeons discriminated the 30° stimuli correctly, while they preferred the negative stimuli with the 0° view and there was no preference for either positive or negative stimuli with the 90° view. One possible explanation for this pattern could be the varying visibility of the heads' appendages in the photographs: The 30° view was the only one where all three appendages of both heads were clearly visible, while at 0° only two appendages of Greeble 1's head were

visible, and one of the three appendages of the head of Greeble 2 were depicted in a way that made it appear just as a dark spot in the middle of the head (see Appendix). 90° represented the “side view” of the heads, which strongly modified the appearance of the visible appendages and even hid some others. Since both heads were of similar overall form it seems likely that the main distinctive features used by the pigeons were the shape and length of the figures' appendages.

V. GENERAL DISCUSSION

The aim of this study was to test picture-object recognition in pigeons in a rotational invariance task and a complementary information procedure and to compare their results with those of humans. I also tested whether visual experience with the real-life objects alters the performance in object recognition tasks that use 2D representations of these objects.

I found that humans were much faster in learning to discriminate photographs of two different objects on a computer screen than pigeons. Although these objects, called Greebles, are meant to be biologically irrelevant stimuli, most humans compared them to well-known objects, such as apples, bulls' heads, vases, or cacti, and some even assigned them human characteristics, such as "belly" and "waist", or "fat" and "thin". It may be concluded that comparing meaningless or unknown objects to mental representations of known objects facilitates their discrimination. Of course, also the pigeons may have compared the Greebles to known objects, but did not succeed in discriminating them as successfully as humans for other reasons. Humans were generally better than pigeons at discriminating unknown views of the Greebles, and there was no difference in performance between interpolated and extrapolated views for humans. These results point to viewpoint-independent object recognition for humans, i.e. recognition of an object by its features alone, regardless of the angle at which it is seen. Pigeons were generally able to discriminate the Greebles even in unfamiliar views, but were significantly better at discriminating interpolated than extrapolated views. This suggests viewpoint-dependent object recognition, meaning that each new view was compared to the mental representation of the closest training view, which made it easier for the birds to discriminate test views that were closer to training views. The same result, i.e. easier discrimination of interpolated views, has been found in many other studies using

pigeons as test subjects (e.g. Bülthoff and Edelman, 1992; Friedman et al., 2005; Srinivas and Schwoebel, 1998).

By means of a complementary information procedure I tried to find out whether pigeons were able to recognize the photographs of the Greebles' trunks used in training as representations of the parts of the real-life objects that were constantly present in their aviary. Therefore, I tested whether the pigeons could discriminate photographs of the Greebles' heads. There was no indication of representational insight, but probably a preference for two-dimensional visual features of one of the heads in two birds. This finding contradicts other studies (Aust and Huber, 2006, 2010) which showed that pigeons can correctly discriminate pictures of humans from pictures without humans, even when tested with pictures of human body parts that were not shown in training. A possible explanation for these deviating results might be the biological irrelevance of the stimuli used in the present study, while Aust and Huber worked with pigeons that had extensive contact with humans which involved feeding and handling, thus making humans a biologically relevant stimulus for these birds. Therefore, it would be interesting to do a follow-up study using the same stimuli (Greebles) but making them biologically relevant, for example by associating them with feeding by putting them in the aviary only when food is present, or placing them next to the feeders. This way the pigeons might pay more attention to them, thus forming a (better) mental representation of the objects.

The angle at which the heads were depicted in the photographs seemed to play an important role in discriminating them, as I could show in the second test that used the complementary information procedure, i.e. the size-test. The results of this test suggest that the pigeons used the appendages (which were distorted or made invisible by rotation to different degrees, depending on rotation angle) as main clue to discriminate the two heads.

This again indicates discrimination by simple two-dimensional features of the photographs without recognition of the objects portrayed.

I did not find any differences in performance between pigeons with the real-life Greebles present in their aviary (present study) and pigeons that could see the Greebles only from the neighboring aviary and had visual access to them only from a limited range of views (preliminary study). Therefore, I could not show a facilitating effect of more direct visual exposure to the three-dimensional objects for two-dimensional object recognition for pigeons.

In conclusion the results of the present study show that pigeons as well as humans are able to discriminate unknown rotated views of biologically irrelevant objects. While this discrimination is viewpoint-dependent for pigeons it seems to be viewpoint-independent for humans. The pigeons in this study were not able to recognize previously missing parts of the objects and there was no difference in performance between pigeons with more direct or indirect visual contact with the objects. Therefore, there was no indication that these birds recognized what they saw on the computer screens as representations of the three-dimensional objects in the aviary. In the preliminary study the pigeons trained with real objects and holograms performed much better than the computer screen-group. It was assumed that this difference in performance might be caused by the latter group not living in the aviary with the real Greebles but in the adjacent aviary, thus having only limited visual contact to them. The present study showed that even when living in the aviary containing the real objects the pigeons' performance does not differ when two-dimensional computer screen stimuli are used. Therefore, the difference in performance of the three groups in the preliminary study seems to be caused by the stimulus type (2D vs. 3D) and not by the degree of visual contact with the real objects.

VI. REFERENCES

Aust, U. and Huber, L. (2006). Picture-object recognition in pigeons: Evidence of representational insight in a visual categorization task using a complementary information procedure. *Journal of Experimental Psychology: Animal Behavior Processes*, 32(2), 190-195.

Aust, U. and Huber, L. (2010). Representational insight in pigeons: comparing subjects with and without real-life experience. *Animal Cognition*, 13, 207-218.

Aust, U. and Steurer, M.M. (2013). Learning of an oddity rule by pigeons in a four-choice touch-screen procedure. *Animal Cognition*, 16, 321-341.

Bayne, K.A. and Davis, R.T. (1983). Susceptibility of rhesus monkeys (*Macaca mulatta*) to the Ponzo illusion. *Bulletin of the Psychonomic Society*, 21(6), 476-478.

Biederman, I. (1987). Recognition-by-Components: A theory of human image understanding. *Psychological Review*, 94(2), 115-147.

Biederman, I. and Gerhardstein, P.C. (1993). Recognizing depth-rotated objects: Evidence and conditions for three-dimensional viewpoint invariance. *Journal of Experimental Psychology: Human Perception and Performance*, 19(6), 1162-1182.

Biederman, I. and Gerhardstein, P.C. (1995). Viewpoint-dependent mechanisms in visual object recognition: Reply to Tarr and Bülthoff (1995). *Journal of Experimental Psychology: Human Perception and Performance*, 21(6), 1506-1514.

Boysen, S.T. and Berntson, G.G. (1986). Cardiac correlates of individual recognition in the chimpanzee (*Pan troglodytes*). *Journal of Comparative Psychology*, 100(3), 321-324.

Boysen, S.T. and Berntson, G.G. (1989). Conspecific recognition in the chimpanzee (*Pan troglodytes*) cardiac responses to significant others. *Journal of Comparative Psychology*, 193(3), 215-220.

Bülthoff, H.H. and Edelman, S. (1992). Psychophysical support for a two-dimensional view interpolation theory of object recognition. *Proceedings of the National Academy of Sciences of the United States of America*, 89, 60-64.

Cabe, P.A. (1976). Transfer of discrimination from solid objects to pictures by pigeons: A test of theoretical models of pictorial perception. *Perception & Psychophysics*, 19(6), 545-550.

Cavoto, B.R. and Cook, R.G. (2006). The contribution of monocular depth cues to scene perception by pigeons. *Psychological Science*, 17, 628-634.

Clement, T.S. and Zentall, T.R. (2003). Choice based on exclusion in pigeons. *Psychonomic Bulletin & Review*, 10(4), 959-964.

Cole, P.D. and Honig, W.K. (1994). Transfer of a discrimination by pigeons (*Columba livia*) between pictured locations and the represented environments. *Journal of Comparative Psychology*, 108(2), 189-198.

Cook, R.G., Qadri, M.A.J., Kieres, A., and Commons-Miller, N. (2012). Shape from shading in pigeons. *Cognition*, 124, 284-303.

Cuthill, I.C. and Bennett, A.T.D. (1993). Mimicry and the eye of the beholder. *Proceedings of the Royal Society B: Biological Sciences*, 253, 203-204.

Cuthill, I.C., Partridge, J.C., Bennett, A.T.D., Church, S.C., Hart, N.S., and Hunt, S. (2000). Ultraviolet vision in birds. *Advances in the Study of Behavior*, 29, 159-214.

Dasser, V. (1987). Slides of group members as representations of the real animals (*Macaca fascicularis*). *Ethology*, 76(1), 65-73.

Dawkins, M.S., Guilford, T., Braithwaite, V.A., and Krebs, J.R. (1996). Discrimination and recognition of photographs of places by homing pigeons. *Behavioural Processes*, 36, 27-38.

D'Eath, R.B. (1998). Can video images imitate real stimuli in animal behaviour experiments? *Biological Reviews*, 73, 267-292.

Delius, J.D., Perchard, R.J., and Emmerton, J. (1976). Polarized light discrimination by pigeons and an electroretinographic correlate. *Journal of Comparative and Physiological Psychology*, 90(6), 560-571.

Deregowski, J.B. (1989). Real space and represented space: Cross-cultural perspectives. *Behavioral and Brain Sciences*, 12, 51-119.

Deregowski, J.B. (2000). Pictorial perception: Individual and group differences within the human species. In Fagot, J. (Ed.) *Picture perception in animals*. (397-429). East Sussex: Psychology Press Ltd.

Deregowski, J.B. and Jahoda, G. (1975). Efficacy of objects, pictures and words in a simple learning task. *International Journal of Psychology*, 10(1), 19-25.

Dittrich, L., Adam, R., Ünver, E., and Güntürkün, O. (2010). Pigeons identify individual humans but show no sign of recognizing them in photographs. *Behavioural Processes*, 83, 82-89.

Diwadkar, V.A. and McNamara, T.P. (1997). Viewpoint dependence in scene recognition. *Psychological Science*, 8, 302-307.

Dyer, A.G. and Voung, Q.C. (2008). Insect brains use image interpolation mechanisms to recognise rotated objects. *PLoS ONE* 3(12): e4086. doi:10.1371/journal.pone.0004086

Edelman, S. and Bülthoff, H.H. (1992). Orientation dependence in the recognition of familiar and novel views of three-dimensional objects. *Vision Research*, 32(12), 2385-2400.

Emmerton, J. and Delius, J.D. (1980). Wavelength discrimination in the 'visible' and ultraviolet spectrum by pigeons. *Journal of Comparative Physiology*, 141, 47-52.

Fagot, J., Martin-Malivel, J., and Dépy, D. (2000). What is evidence for an equivalence between objects and pictures in birds and nonhuman primates? In Fagot, J. (Ed.) *Picture perception in animals*. (295-320). East Sussex: Psychology Press Ltd.

Friedman, A., Spetch, M.L., and Ferrey, A. (2005). Recognition by humans and pigeons of novel views of 3-D objects and their photographs. *Journal of Experimental Psychology: General 2005*, 134(2), 149-162.

Fujita, K., Blough, D.S., and Blough, P.M. (1991). Pigeons see the Ponzo illusion. *Animal Learning & Behavior*, 19(3), 283-293.

Fujita, K., Blough, D.S., and Blough, P.M. (1993). Effects of the inclination of context lines on perception of the Ponzo illusion by pigeons. *Animal Learning & Behavior*, 21(1), 29-34.

Gauthier, I. and Tarr, M.J. (1997). Becoming a "Greeble" expert: Exploring mechanisms for face recognition. *Vision research*, 37(2), 1673-1682.

Goodale, M.A. (1983). Visually guided pecking in the pigeon (*Columba livia*). *Brain, Behavior and Evolution*, 22, 22-41.

Grabner, V. (2010). Influence of familiarity with a category on picture-object recognition in pigeons *(Columba livia).* Master's thesis

Hayward, W.G. and Tarr, M.J. (1997). Testing conditions for viewpoint invariance in object recognition. *Journal of Experimental Psychology: Human Perception and Performance*, 23(5), 1511-1521.

Hayward, W.G. and Williams, P. (2000). Viewpoint dependence and object discriminability. *Psychological Science*, 11(7), 7-12.

Herrnstein, R.J., Loveland, D.H., and Cable, C.J. (1976). Natural concepts in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes*, 2, 285-302.

Hollard, V.D. and Delius, J.D. (1982). Rotational invariance in visual pattern recognition by pigeons and humans. *Science*, 218, 804-806.

Husband, S. and Shimizu, T (2001). Evolution of the avian visual system. In R. G. Cook (Ed.), *Avian visual cognition* [On-line].
Available: www.pigeon.psy.tufts.edu/avc/husband/

James, T.W., Shima, D.W., Tarr, M.J., and Gauthier, I. (2005). Generating complex three-dimensional stimuli (Greebles) for haptic expertise training. *Behavior Research Methods*, 37(2), 353-358.

Kumar, S. and Hedges, B. (1998). A molecular timescale for evolution. *Nature,* Vol.392(30), 917-920.

Lang, P.J., Bradley, M.M., and Cuthbert, B.N. (1998). Emotion, motivation, and anxiety: Brain mechanisms and psychophysiology. *Biological Psychiatry*, 44, 1248-1263.

Lechelt, D.P. and Spetch, M.L. (1997). Pigeons' use of landmarks for spatial search in a laboratory arena and in digitized images of the arena. *Learning and Motivation*, 28, 424-445.

Loidolt, M., Aust, U., Meran, I., and Huber, L. (2003). Pigeons use item-specific and category-level information in the identification and categorization of human faces. *Journal of Experimental Psychology: Animal Behavior Process*es, 29(4), 261-276.

Looney, T.A. and Cohen, P.S. (1974). Pictorial target control of schedule-induced attack in white carneaux pigeons. *Journal of the Experimental Analysis of Behavior*, 21, 571-584.

McFadden, S.A. (1993). Constructing the three-dimensional image. In Zeigler, H.P. and Bischof, H.J. (Eds.), *Vision, brain, and behaviour in birds*. (47-61). Cambridge, MA: MIT Press.

Nakamura, N., Watanabe, S., and Fujita, K. (2009). Further analysis of perception of the standard Müller-Lyer figures in pigeons (*Columba livia*) and humans (*Homo sapiens*): Effects of length of brackets. *Journal of Comparative Psychology*, 123(3), 287-294.

Parron, C., Call, J., and Fagot, J. (2008). Behavioural responses to photographs by pictorially naïve baboons (*Papio anubis*), gorillas (*Gorilla gorilla*) and chimpanzees (*Pan troglodytes*). *Behavioural Processes*, 78, 351-357.

Peissig, J.J., Wasserman, E.A., Young, M.E., and Biederman, I. (2002). Learning an object from multiple views enhances its recognition in an orthogonal rotational axis in pigeons. *Vision Research*, 42, 2051-2062.

Peissig, J.J., Young, M.E., Wasserman, E.A., and Biederman, I. (2000). The pigeon's perception of depth-rotated shapes. In Fagot, J. (Ed.) *Picture perception in animals*. (295-320). East Sussex: Psychology Press Ltd.

Reid, S.L. and Spetch, M.L. (1998). Perception of pictorial depth cues by pigeons. *Psychonomic Bulletin & Review*, 5(4), 698-704.

Remy, M. and Emmerton, J. (1989). Behavioral spectral sensitivities of different retinal areas in pigeons. *Behavioral Neuroscience*, 103(1), 170-177.

Rock, I. and DiVita, J. (1987). A case of viewer-centered object perception. *Cognitive Psychology*, 19(2), 280-293.

Romeskie, M. and Yager, D. (1976). Psychophysical studies of pigeon color vision – I. Photopic spectral sensitivity. *Vision Research*, 16, 501-505.

Shimizu, T. (1998). Conspecific recognition in pigeons (*Columba livia*) using dynamic video images. *Behaviour*, 135(1), 43-53.

Slater, A., Morison, V., and Rose, D. (1984). New-born infants' perception of similarities and differences between two- and three-dimensional stimuli. *British Journal of Developmental Psychology*, 2(4), 287-294.

Spetch, M.L. and Friedman, A. (2003). Recognizing rotated views of objects: Interpolation versus generalization by humans and pigeons. *Psychonomic Bulletin & Review*, 10(1), 135-140.

Spetch, M.L. and Friedman, A. (2006). Pigeons see correspondence between objects and their pictures. *Psychological Science*, 17, 966-972.

Spetch, M.L., Kelly, D.M., and Lechelt, D.P. (1998). Encoding of spatial information in images of an outdoor scene by pigeons and humans. *Animal Learning & Behavior*, 26(1), 85-102.

Spetch, M.L., Kelly, D.M., and Reid, S. (2000). Recognition of objects and spatial relations in pictures across changes in viewpoint. In Fagot, J. (Ed.) *Picture perception in animals*. (107-141). East Sussex: Psychology Press Ltd.

Srinivas, K. and Schwoebel, J. (1998). Generalization of novel views from view combination. *Memory & Cognition*, 26(4), 768-779.

Stephan, C., Steurer, M.M., and Aust, U. Discrimination of holograms and real objects by pigeons and humans. Submitted to *Journal of Comparative Psychology.*

Stephan, C., Wilkinson, A., and Huber, L. (2013). Pigeons discriminate objects on the basis of abstract familiarity. *Animal Cognition* (2013), 1-10.

Steurer, M.M., Aust U., and Huber, L. (2012). The Vienna comparative cognition technology (VCCT): An innovative operant conditioning system for various species and experimental procedures. *Behaviour Research*, 44, 909-918.

Tarr, M.J. (1995). Rotating objects to recognize them: A case study on the role of viewpoint dependency in the recognition of three-dimensional objects. *Psychonomic Bulletin & Review*, 2(1), 55-82.

Tarr, M.J. and Bülthoff, H.H. (1995). Is human object recognition better described by geon structural descriptions or by multiple views? Comment on Biederman and Gerhardstein (1993). *Journal of Experimental Psychology: Human Perception and Performance*, 21(6), 1494-1505.

Tarr, M.J. and Pinker, S. (1989). Mental rotation and orientation-dependence in shape recognition. *Cognitive Psychology*, 21, 233-282.

Timney, B. and Keil, K. (1996). Horses are sensitive to pictorial depth cues. *Perception*, 25(9), 1121-1128.

Ullman, S. (1989). Aligning pictorial descriptions: An approach to object recognition. *Cognition*, 32(3), 193-254.

Vaughan, W.Jr. and Greene, S.L. (1984). Pigeon visual memory capacity. *Journal of Experimental Psychology: Animal Behavior Processes*, 10(2), 256-271.

Walls, G.L. (1942). *The vertebrate eye and its adaptive radiation*. Bloomfield Hills, Mich.: Cranbrook Institute of Science.

Wasserman, E.A., Gagliardi, J.L., Cook, B.R., Kirkpatrick-Steger, K., Astley, S.L., and Biederman, I. (1996). The pigeon's recognition of drawings of depth-rotated stimuli. *Journal of Experimental Psychology: Animal Behavior Process*es, 22(2), 205-221.

Watanabe, S. (1997a). An instance of viewpoint consistency in pigeon object recognition. *Behavioural Processes*, 39, 257-261.

Watanabe, S. (1997b). Visual discrimination of real objects and pictures in pigeons. *Animal Learning & Behavior*, 25(2), 185-192.

Watanabe, S. (1999). Enhancement of viewpoint invariance by experience in pigeons. *Cahiers de Psychologie Cognitive/Current Psychology of Cognition*, 18(3), 321-335.

Watanabe, S., Lea, S.E.G., and Dittrich, W.H. (1993). What can we learn from experiments on pigeon concept discrimination? In Zeigler, H.P. and Bischof, H.J. (Eds.), *Vision, brain, and behaviour in birds*. (47-61). Cambridge, MA: MIT Press.

Wilkie, D.M., Willson, R.J., and Kardal, S. (1989). Pigeons discriminate pictures of a geographic location. *Animal Learning & Behavior*, 17(2), 163-171.

VII. APPENDIX

Table 7: Number of sessions to criterion (successful discrimination between positive and negative stimuli in four out of five consecutive sessions) for all subjects in the present and in the preliminary study.

	Subject	Exp. Group	Sessions to criterion
Pigeons present study	Art	G1	61
	Electra	G1	68
	Lukas	G1	66
	Ron	G1	60
	Azurro	G2	85
	Hermine	G2	16
	Perdita	G2	179
	Steve	G2	31
	Vesper	G2	187
	Mean ±SD		83.7 ±59.95
Humans present study	H1	G1	4
	H2	G1	4
	H3	G1	4
	H4	G1	4
	H5	G1	4
	H6	G1	4
	H7	G2	4
	H8	G2	4
	H9	G2	7
	H10	G2	5
	H11	G2	5
	Mean ±SD		4.5 ±0.93
Pigeons preliminary study	Franz	G1	190
	Klara	G1	145
	Ferdinand	G1	60
	Cordula	G2	45
	Josef	G2	70
	Birgit	G2	125
	Meggie	G2	95
	Mean ±SD		104.3 ±51.92

Note: Experimental group G1 refers to individuals being trained to respond to Greeble 1, experimental group G2 refers to individuals being trained to respond to Greeble 2. Sessions to criterion indicates the number of training session required to reach the criterion of mastery.

Fig.17: Stimuli used in discrimination training (not actual size).

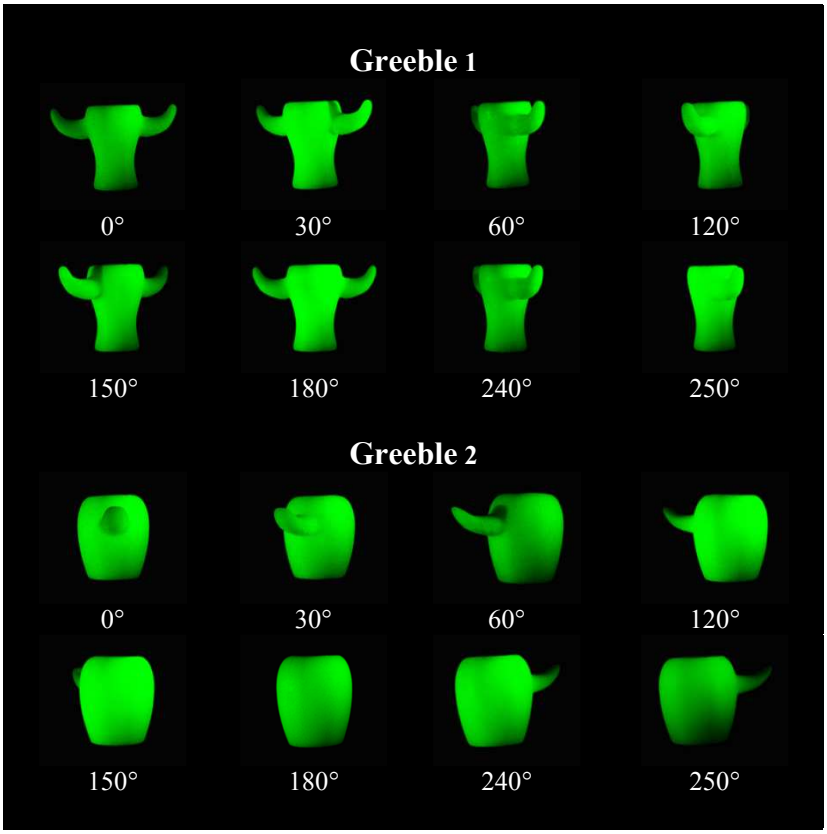


Fig.18: Test stimuli used in the rotational invariance test (not actual size).

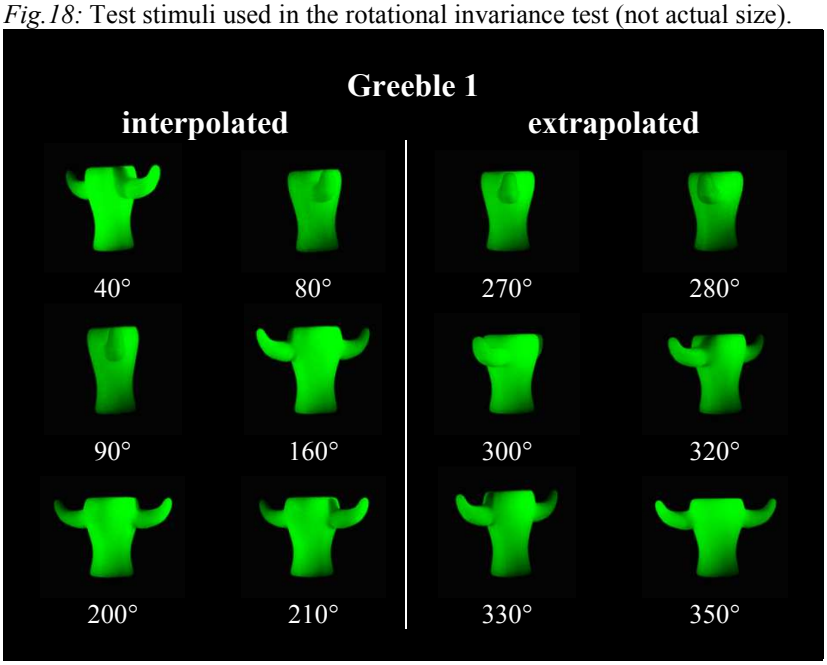


Fig.18: Test stimuli used in the rotational invariance test (not actual size) (continued).

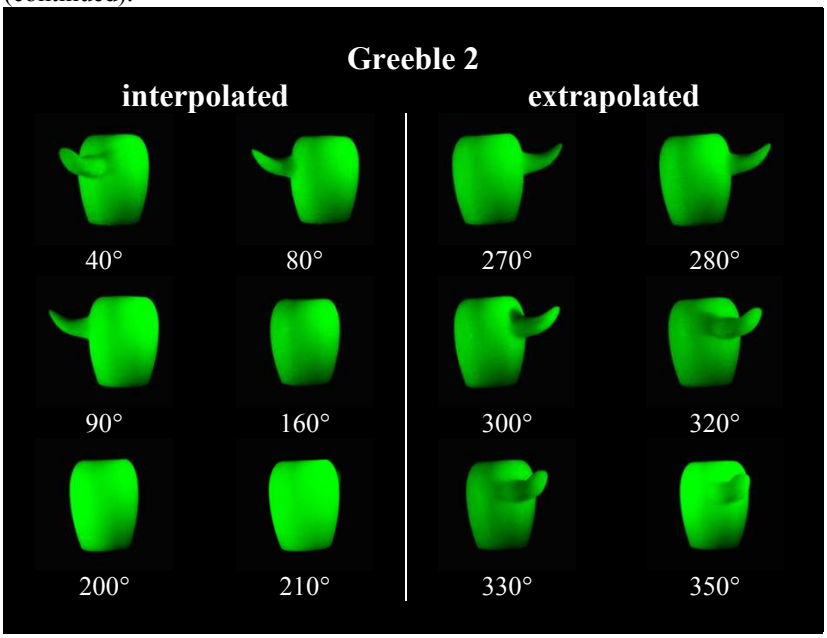


Fig.19: Test stimuli used in the head-test (not actual size).

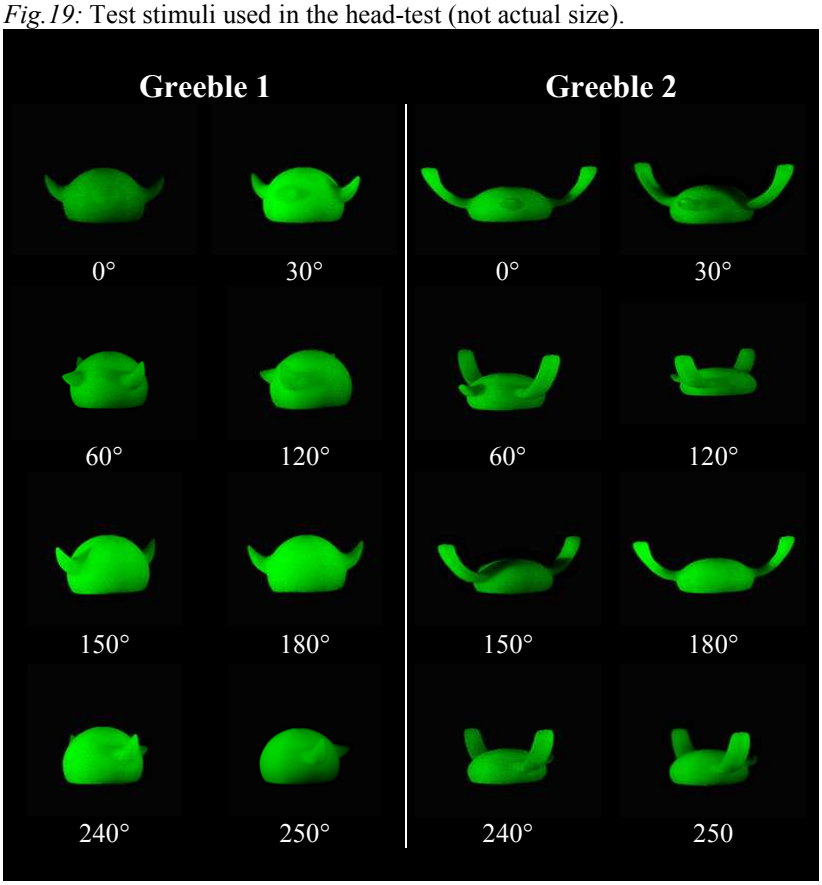
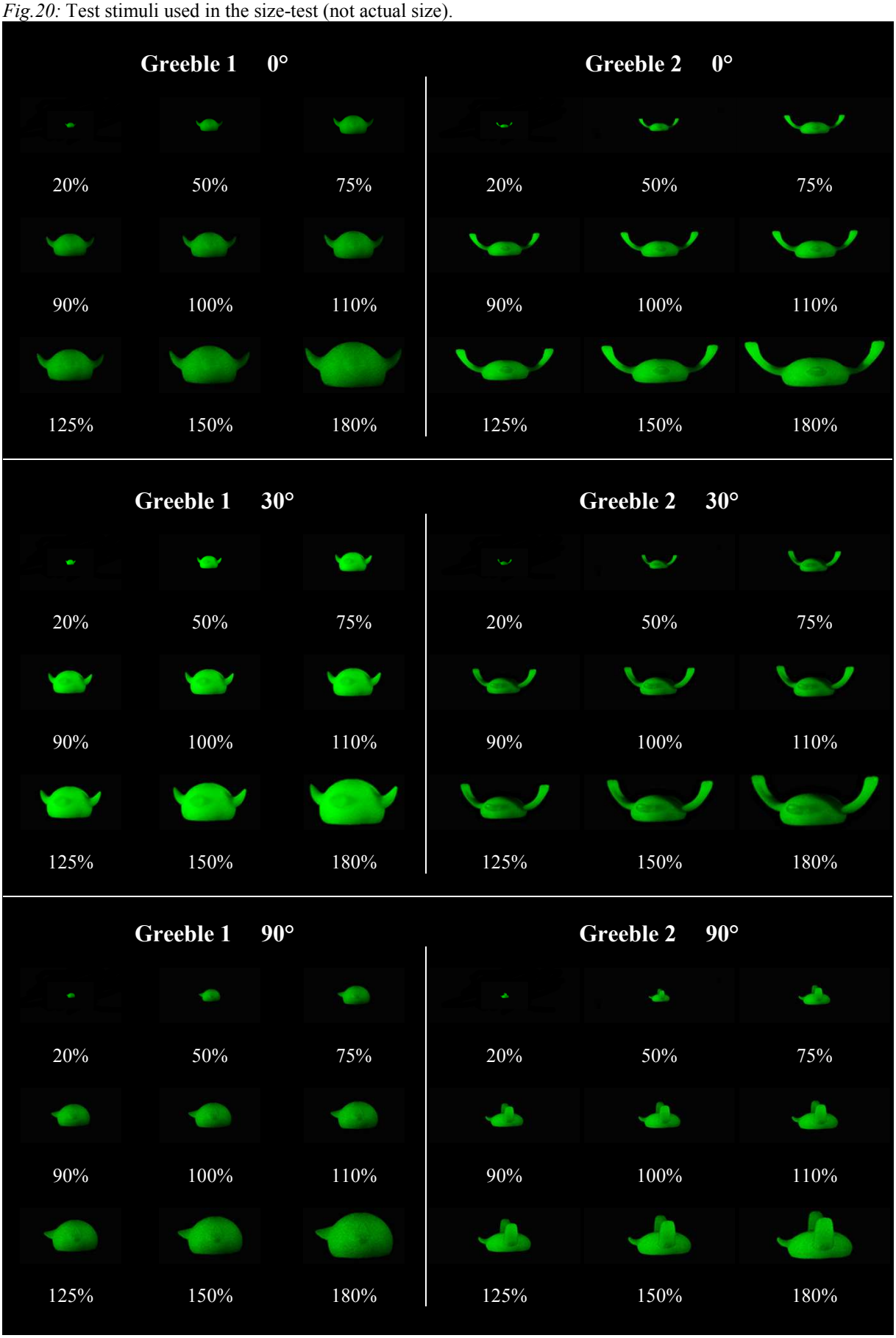


Fig.20: Test stimuli used in the size-test (not actual size).



Fragebogen:

Der Vergleich zwischen Menschen und Tauben am Bildschirm

Information

Du wirst an einem Experiment teilnehmen, in dem es um visuelles Unterscheiden geht. Mittels einer klassischen Go/no-go Prozedur wird deine Reaktion digital aufgezeichnet. Du wirst gebeten, zwischen verschiedenen Stimuli visuell zu unterscheiden, die entweder als positive oder negativ vom Experimentator definiert wurden. Nach einer anfänglichen Trainingsphase, in der du diese Unterscheidung erlernst, schließt sich eine Testphase an.

Bitte gib deine jeweilige Einschätzung durch das Klicken der Maus an. Wenn du glaubst, der präsentierte Stimulus ist als positiv definiert, drücke bitte die Maus mindestens 2Mal/Sekunde sobald er erscheint bis der Stimulus wieder verschwindet. Falls du denkst, ein negativer Stimulus wird präsentiert, betätige die Maus bitte nicht bis der Stimulus wieder verschwindet. Solltest du dir unsicher sein, ob der präsentierte Stimulus positiv oder negativ ist, versuche auch deine Unschlüssigkeit durch das Klicken der Maus zu kodieren (weniger als auf sicher positive, doch mehr als auf sicher negative Stimuli).

Deine Ergebnisse werden nachfolgend mit jenen der Tauben verglichen, die das gleiche Experiment absolvieren.

Deine persönlichen Angaben sowie deine Ergebnisse werden anonym behandelt.

Bist du an einer zusammenfassenden Präsentation des Taube – Mensch Vergleiches interessiert?

☐ ja ☐ nein

Persönliche Angaben

Vorname: _____

Nachname: _____

Alter: _____

☐ männlich ☐ weiblich

Kontaktinformation (E-Mail Adresse oder Telefonnummer):

_____

Fragen

Schätzt du die Aufgabe als leicht zu bewältigen ein?

☐ ja ☐ nein; warum?:

Wie glaubst du zwischen positiven und negativen Stimuli unterschieden zu haben?

☐ anhand der Farbe

☐ anhand der Größe

☐ anhand von Symmetrie

☐ anhand der generellen Form; welche Teile oder Charakteristika genau?:

☐ andere; welche?

Vielen Dank für deine Teilnahme!

☐ ich stimme der anonymen Veröffentlichung meiner Versuchsergebnisse zu.

Datum, Unterschrift

ABSTRACT

Pigeons and humans are two highly visual species that have evolved separately for about 310 million years (Kumar and Hedges, 1998) and developed largely convergent visual systems due to similar visual needs. To investigate pigeon vision and cognitive abilities two-dimensional pictorial stimuli are often used. However, it is not entirely clear, how pigeons perceive such stimuli and whether or not they can associate photographs with real objects.

In the present study nine pigeons and eleven humans were trained to discriminate between photographs of two biologically irrelevant objects ("Greebles"). The pigeons were housed in an aviary containing the real Greebles and were trained in wooden chambers where they had to peck on a Plexiglas disk when positive stimuli were presented, thus obtaining food. Humans were trained with the same stimuli presented on a computer screen and had to click with a computer mouse on positive stimuli. Results showed that humans were much faster at learning to discriminate the two Greebles. In the first test, pigeons and humans had to discriminate new rotational views of the Greebles. Humans performed equally well on interpolated test views (i.e. views that lay between the training views) and extrapolated views (i.e. views outside of training range), while pigeons performed better on interpolated than on extrapolated test views. Therefore, it can be concluded that object recognition was viewpoint-independent for humans and viewpoint-dependent for pigeons. In the second test, following a procedure by Aust and Huber (2006), pigeons were presented with parts of the Greebles that were not included in training and the first test to see whether they formed associations between the 2D images and the 3D objects in their aviary. They did not discriminate these parts correctly. The test was repeated with three of the test views already used in the second test but presented in different sizes. Discrimination seemed to depend on the visibility of the appendages and might have been based on visual features of the pictures themselves without

recognition of what they portrayed. The results of this study were compared to a previous study in which pigeons were trained to discriminate either real Greebles, holograms, or computer images of them. There, too, the real Greebles were installed in the pigeons' aviary; however, the pigeons trained and tested on computer images lived in the adjacent aviary and thus only had limited visual contact to them. We wanted to find out whether the more extensive visual contact to the Greebles had any influence on the pigeons' performance. However, there was no difference in performance between the two groups. This is evidence that the result of the previous study — better performance with real objects and holograms than with computer images — was not based on the fact that pigeons trained with the latter stimulus type had only limited visual access to the real 3D objects.

ZUSAMMENFASSUNG

Tauben und Menschen sind zwei hochvisuelle Spezies, deren Evolution seit circa 310 Millionen Jahren getrennt verläuft (Kumar und Hedges, 1998). Da sie ähnliche visuelle Anforderungen haben entwickelten sie konvergente visuelle Systeme. Um das Sehvermögen und kognitive Fähigkeiten von Tauben zu untersuchen werden oft zweidimensionale Stimuli benutzt. Es ist jedoch nicht restlos geklärt, wie Tauben diese Stimuli wahrnehmen und ob sie Fotografien als Repräsentationen von echten Objekten erkennen.

In der vorliegenden Studie wurden neun Tauben und elf Menschen darauf trainiert, Fotos von zwei biologisch irrelevanten Objekten („Greebles“) zu unterscheiden. Die Tauben lebten während des Versuches in einer Voliere, in welcher die echten Greebles angebracht waren. Sie wurden in Holzkammern trainiert, wo sie auf Plexiglasscheiben picken mussten, wenn ein positiver Stimulus am Bildschirm erschien, um eine Belohnung in Form von Futter zu bekommen. Menschen wurden mit denselben Stimuli präsentiert auf einem Computerbildschirm trainiert, auf die sie mit einer Maus klicken mussten. Menschen erlernten die Unterscheidung wesentlich schneller als Tauben. Im ersten Test mussten Tauben und Menschen unbekannte Ansichten der Greebles richtig unterscheiden. Bei Menschen bestand kein Unterschied zwischen interpolierten (d.h. Ansichten, die zwischen den Trainingsansichten liegen) und extrapolierten Testansichten (d.h. Ansichten außerhalb der Trainingsansichten), während Tauben interpolierte Testansichten besser als extrapolierte unterschieden. Daher kann man darauf schließen, dass die Objekterkennung für Menschen unabhängig vom Ansichtswinkel und für Tauben abhängig vom Ansichtswinkel war. Im zweiten Test wurden den Tauben nach einer Prozedur von Aust und Huber (2006) Teile der Greebles präsentiert, die nicht im Training und dem ersten Test verwendet wurden, um festzustellen, ob sie zwischen den zweidimensionalen Bildern und den dreidimensionalen

Objekten Assoziationen gebildet hatten. Es gab jedoch kein Anzeichen dafür, dass dies der Fall war. Der Test wurde mit drei Testansichten aus dem zweiten Test wiederholt, die jedoch in verschiedenen Größen präsentiert wurden. Die Unterscheidung der Objekte schien von der Sichtbarkeit der Körperanhänge abzuhängen und könnte durch visuelle Eigenschaften der Bilder selbst verursacht sein, ohne, dass die Tauben erkannten, was auf ihnen dargestellt wird. Die Ergebnisse der vorliegenden Studie wurden außerdem mit einer vorangegangenen Studie verglichen. In dieser Studie wurden Tauben mit den echten Greebles, Hologrammen oder zweidimensionalen Bildern trainiert. Die Tauben lebten auch hier in einer Voliere, in der die Greebles angebracht waren; allerdings galt dies nur für die echten Greebles- und Hologramm-Gruppen. Die Bildschirm-Gruppe lebte in der Nachbarvoliere und hatte daher nur eine eingeschränkte Sicht auf die Greebles. Daher wollten wir herausfinden, ob mehr visuelle Erfahrung mit den Objekten deren Unterscheidung auf Fotos erleichtert. Es gab jedoch keine Unterschiede in der Leistung der beiden Gruppen. Daher kann man annehmen, dass die Resultate der vorangegangenen Studie – nämlich, dass Tauben bessere Leistung mit echten Objekten und Hologrammen zeigten als mit Computerbildern – nicht auf der Tatsache beruht, dass diese Tauben nur limitierten visuellen Kontakt zu den 3D Objekten hatten.

CURRICULUM VITAE

Personal information

Name	Mag. Anna Frohnwieser
Date of birth	27.04.1987
Nationality	Austria
Address	Rueppgasse 38/21
	1020 Vienna
	Austria
Mobile	+4369911801386
E-Mail	annafrohnwieser@hotmail.com

Education

1993 – 1997	Volksschule St. Margarethen/Bgld.
1997 – 2000	BG/BRG/BORG Eisenstadt
2000 – 2005	BG und BRG Neusiedl am See
June, 7th 2005	Graduation with distinction

October 2005 – July 2007	Undergraduate studies in Biology at the University of Vienna
Since July 2007	Studies of Anthropology and Zoology, University of Vienna
2010 – 2012	Diploma Thesis: "Human walking behavior – The effect of density on walking speed and direction", Department of Anthropology, University of Vienna Referee: A.o. Univ.-Prof. Dr. Karl Grammer
June, 21st 2012	Graduation (Mag[a].rer.nat.) with honors
Since Oct. 2011	Diploma Thesis: "Picture-object recognition in a comparative approach: Performance of humans and pigeons (*Columba livia*) in a rotational invariance and a complementary information task", Department of Cognitive Biology, University of Vienna Referee: Dr. Ulrike Aust

---

Talks

Frohnwieser, A., Oberzaucher, E., Grammer, K., and Hopf, R. (2012). Human walking behavior - The effect of density on walking speed and direction. XXI Biennial Conference on Human Ethology (ISHE), Vienna, Austria

Publications

Frohnwieser, A., Hopf, R., and Oberzaucher, E. (2013). Human Walking Behavior – The Effect of Pedestrian Flow and Personal Space Invasions on Walking Speed and Direction. *Human Ethology Bulletin,* 28(3), 20-28.